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Morphological and Anatomical Considerations of the Grass Subfamily Bambusoideae Based on the New Genus *Maclurolyra*

CLEOFÉ E. CALDERÓN
and
THOMAS R. SODERSTROM

SMITHSONIAN CONTRIBUTIONS TO BOTANY · NUMBER 11

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ABSTRACT

Calderón, Cleofé E., and Thomas R. Soderstrom. Morphological and Anatomical Considerations of the Grass Subfamily Bambusoideae Based on the New Genus *Maclurolyra. Smithsonian Contributions to Botany,* number 11, 55 pages, 24 figures, 1973.—*Maclurolyra tecta,* a new genus of grasses from Panama, is described. Features of its leaf anatomy and epidermis, seedlings, inflorescence morphology, floral structure, and cytology, indicate that it is a member of the tribe Olyreae of the subfamily Bambusoideae. A description is given of the "bambusoid" type of leaf anatomy, as well as comments on the vascular bundle sheaths in grasses, and chloroplast structure and photosynthetic pathways as new criteria in grass taxonomy. The phylogenetic position of *Maclurolyra* is discussed and a list of genera comprising the Bambusoideae is presented.

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Introduction

Accounts of the great diversity of species that are found in tropical rain forests are common, but mostly these are based on inventories of the trees that are the conspicuous element of this biome. Less attention has been paid to the herbaceous vegetation of the understory where the decrease in illumination, change in light quality, and relatively high humidity create conditions which are hostile to most plants. The majority of herbaceous plants that thrive under such conditions in the rain forests of tropical America belong to relatively few families—Araceae, Bromeliaceae, Commelinaceae, Marantaceae, Musaceae, Orchidaceae, Zingiberaceae. Although they do not constitute a significant part of this understory vegetation, either in number of species or in individuals, representatives of the grass family also occur here.

The new genus that we are describing here occurs in Panama where it has so far been located in forests of two areas—Santa Rita, on the Atlantic slope, and Cerro Jefe, on the Pacific slope (Figure 1). Lumbering trails have afforded botanists the opportunity to reach areas of virgin forest previously inaccessible in Panama and *Maclurolyra* is only one of many new plants found in recent years in such forests.

Santa Rita is an area of primary forest situated on an undulating terrain, which is traversed by numerous streams and creeks, and ranges in elevation from about 200 to 450 meters. From April through December heavy rains occur almost daily. Recent collections made in late October and early November, at the peak of the rainy season, showed all plants to be in flower, with some in fruit, and with the presence of many seedlings around the parent clumps. The type-collection was made in early March, at the end of the dry season. At this time the plants were in flower and many old inflorescences were also found. Apparently *Maclurolyra* is in flower throughout the year with the most profuse flowering occurring during the rainy season.

Plants of *Maclurolyra* grow in small clumps scattered throughout the forest, usually around or near trees or under plants of larger size. In some places they grow in association with grasses of the related genus, *Cryptochloa* (Figure 2*a,c*). All of these are found in reddish soil and apparently thrive only where it is shaded and humid. Plants

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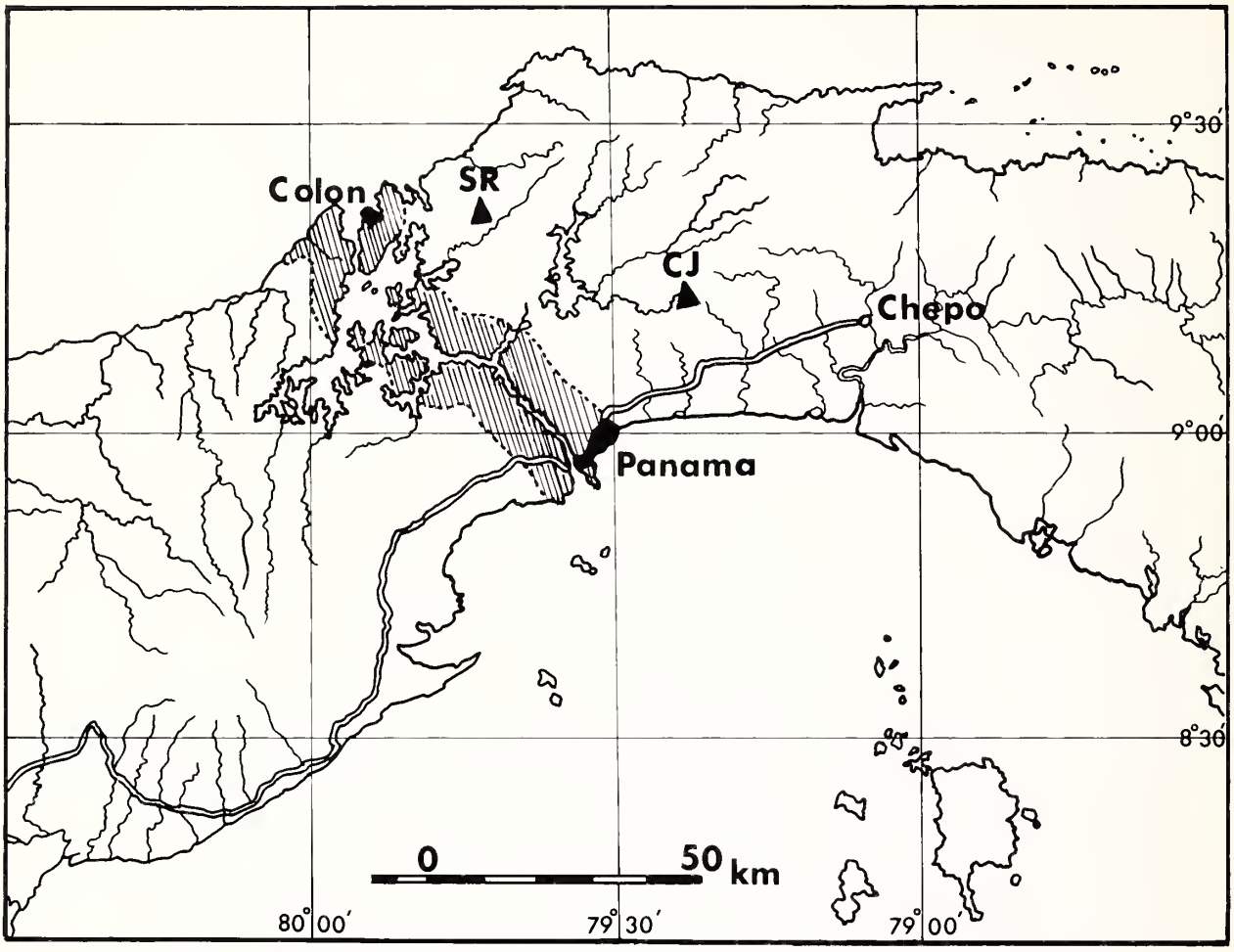


FIGURE 1.—Map of Panama showing localities where *Maclurolyra tecta* has been collected: [*SR*=Santa Rita, *CJ*=Cerro Jefe, cross-hatched area=Canal Zone].

of *Maclurolyra* left exposed in nearby cut-over areas of forest were found to be stunted and with few, small, poorly developed inflorescences--presumably in response to the intense illumination and decrease in humidity. *Maclurolyra* was found also, but in less abundance, in some areas of Cerro Jefe, a forest region on the Pacific slope of Panama. The higher elevation (ca. 800 meters), where cooler and less humid conditions are encountered than at Santa Rita, possibly accounts for the reduction in numbers of plants.

Studies of the morphology and anatomy of this peculiar new genus have revealed that it is related to *Olyra* and grasses of the tribe Olyreae ("olyroid grasses"), which tribe we include in the subfamily Bambusoideae, as had Roshevitz (1946) and Parodi (1961). (For a brief account of the morphology and anatomy of members of this tribe see Calderón and Soderstrom, 1967.) Recently we have discussed the pollination biology of some grasses of the Olyreae, with comments on the relationships of some of these herbaceous grasses to the woody bamboos, all of which we refer to in a general way as "bambusoid grasses" (Soderstrom and Calderón, 1971).

Our studies on the new genus have been made from the standpoint of its morphology and anatomy, with a view not only to elucidating its systematic position within the grass family, but with the objective of clarifying and defining more precisely the "bambusoid type" of leaf anatomy. This allows us the opportunity to present some general considerations on the morphology, anatomy, and taxonomy of the subfamily Bambusoideae,

FIGURE 2.—*Maclurolyra tecta* in the field (Santa Rita forest, Panama): A, Mature plant (indicated by arrow) growing in association with plants of *Cryptochloa*; B, close-up of adult plant; C, close-up of adult plant with a plant of *Cryptochloa* in the background.

including remarks on the tribe Olyreae. We have felt it useful to present at the end of this report a list of all genera which we consider to be members of the subfamily Bambusoideae (Appendix 1).

The genus is named in honor of our late colleague, Floyd A. McClure (1897-1970). We are indebted to him for the countless hours of consultation over the years regarding problems of bamboo morphology. He became familiar with the new genus as we studied it and shared with us, in

FIGURE 3.—Inflorescence of *Maclurolyra tecta* in the field (Santa Rita forest, Panama): A, Newly emerging inflorescence as seen from above; B, inflorescence in front of the blade; C, inflorescence beginning to twist; D, inflorescence at a later stage in back of the blade; E, old inflorescence bent downward in back of a blade (see arrow), and one still in front of the blade; F, inflorescence axis bent downward (see arrow).

its interpretation, the wisdom he had acquired during a lifetime devoted to the study of bamboo.

The specific name derives from the Latin word for "cover," in allusion to the uppermost blade on the flowering culm which covers the inflorescence in umbrella-like fashion, shielding the flowers from the rain (Figure 3).

While lumbering trails such as those at Santa Rita allow us access to such genera as *Maclurolyra,* these trails also signal the imminent destruction of these same forests. The actual site of the type-collection of *Maclurolyra*—primary forest in 1968—was revisited in 1971 and found already cleared—a part of the ecosystem that took so long to evolve destroyed forever. It is incumbent upon us, as biologists, to encourage that parts of these forests be protected so that in the future plants of genera such as *Maclurolyra* can still be found in their natural habitat rather than in herbaria as mere dried records of the past.

Acknowledgments.—We feel our deepest gratitude to our major professors who were responsible for our basic training in agrostology, Professor John R. Reeder (Laramie, Wyoming) and the late Professor Ingeniero Lorenzo R. Parodi (Buenos Aires).

The present study was possible only because of the support and facilities offered by many institutions and offices, and the personal assistance, cooperation, and advice rendered to us by colleagues in the United States, Latin America, Europe, India, and Ceylon. Primary credit is to be given to the Smithsonian Institution, Washington, D.C., for grants from the Smithsonian Research Foundation to the junior author which have provided for the laboratory studies to be carried out. Support for Calderón to travel to Central and South America during 1967-1968 was provided by the Smithsonian's Office of Systematics and Office of Ecology, and for this trip a travel grant was awarded by the Office of Scientific Affairs, Organization of American States. The field work in Panama, during which period the new genus was collected, was possible only because of the assistance given by Dr. Robert L. Dressler (Smithsonian Tropical Research Institute, Balboa, Canal Zone) to whom we are especially indebted. A grant from the Smithsonian's Office of International Activities allowed Calderón to spend some time in Europe on the way to India, and provided the opportunity to discuss matters relating to the new genus with specialists in various institutions. We would like to extend our thanks to Dr. C. R. Metcalfe (Jodrell Laboratory, Royal Botanic Gardens, Kew, England) for his review and criticisms of the anatomical studies of the new genus; and at the herbarium of the Royal Botanic Gardens, Kew, to the renowned agrostologist, Dr. C. E. Hubbard, for his taxonomic suggestions. The morphological discussions concerning grasses, and particularly the inflorescence of the new genus, were made with specialists at the Universität Mainz, West Germany, and particular acknowledgment is made to Prof. Dr. H. Weber (Director, Institut für Spezielle Botanik) and his colleagues at the same University, Profs. Drs. D. Hartl and S. Vogel. We would like to express our very deep gratitude to the eminent morphologist, Prof. Dr. Wilhem Troll, also of Mainz, for the numerous hours he devoted to Calderón in his laboratory, discussing the inflorescence morphology of *Maclurolyra.* His advice, suggestions, and encouragement to continue in the difficult study of grass inflorescence morphology, are all deeply appreciated. We are grateful as well for the advice given by Dr. H. J. Conert (Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt), Dr. H. Jacques-Félix (Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris), Dr. F. Bugnon (Faculté des Sciences de Dijon, France), Dr. G. Bocquet (Institut für Spezielle Botanik, Eidg. Technische Hochschulle, Zürich), and Dr. E. Mora-Osejo (Instituto de Ciencias Naturales, Bogotá). We would like to thank Dr. V. Puri (Meerut University, Meerut, India) for his advice on embryological problems in the Gramineae and his generosity in allowing the use of his laboratory and facilities in India. Dr. Pierre Morisset (Université Laval, Québec) was kind enough to study the chromosomes of the new genus and provide the photograph which appears in Figure 14*d*.

We are grateful to Mrs. Nina Smith (Hunt Botanical Library, Pittsburgh), who assisted in the transliterations of the Russian titles and in translating passages from various Russian and German papers.

We appreciate the suggestions and assistance provided by several colleagues at our own institution—Dr. E. S. Ayensu, Dr. José Cuatrecasas, Dr. Mason E. Hale, Jr., the late Mr. Conrad V. Morton, Dr. Lyman B. Smith and Dr. William L. Stern.

We were fortunate to have the habit drawings

prepared by our illustrator, Mrs. Gesina Berendina Threlkeld (GBT) of Delta, Alaska, and a few of the sketches by Mr. Christopher Reinecke (CR) of Washington, D.C.

Materials and Methods.—Plants were collected in the field and herbarium specimens prepared in the usual fashion by placing them between newspapers in a plant press and drying with supplementary heat. Living plants were collected in the area of Santa Rita in October 1971 and taken to Washington, D.C., where they are under cultivation in a greenhouse.

Field photographs were taken with a Nikon F camera (equipped with a Nikon Photomic-TN Finder), using the Micro-Nikkor 55mm lens and Kodak Tri-X film (ASA 400), without an additional light source. A tripod was used in all instances.

Material for morphological, anatomical, and cytological studies was fixed in the field at time of collection. For cytological studies young inflorescences were fixed in a mixture of three parts 95 percent EtOH to one part glacial acetic acid, and transferred within 24 hours to 70 percent EtOH and stored under refrigeration. Inflorescences, leaves, and seedlings were fixed in FAA (5 cc formalin: 5 cc glacial acetic acid: 90 cc of 50% EtOH). The blade of the first or second completely developed leaf from the uppermost part of the culm was selected for preservation. Young inflorescences were also fixed, in a mixture consisting of equal parts of glycerine and lactic acid (Bersier and Bocquet, 1960).

Studies of the leaf anatomy were made on material preserved in FAA. After washing, the sections were cut by hand with a razor blade from the middle portion of the blade, and mounted, without staining, in glycerine or glycerine-lactic acid.

Preparations of epidermises of the leaves were made by the standard technique of scraping and mounted, without staining, in glycerine. Some preparations were stained with a weak solution of safranin, without dehydration, to facilitate the observation of the siliceous cells and microhairs.

The gynoecia were dissected and mounted, without staining, in glycerine-lactic acid and studied with phase contrast and dark field illumination. The glycerine-lactic acid mixture acts not only as a good clearing agent but preservative as well and the material needs no further transferring after fixing in the field. Flowers treated in this way are the most suitable for studies under phase contrast and polarized light. Flowers so treated were used in the studies of the venation of glumes, lemmas, and paleas, and the vascular traces of the gynoecium. These parts were mounted in the same clearing agent. The ovule structure was also studied from material in this preservative.

Herbarium material, when used in dissection, was treated with "Aerosol OT Solution" (Fischer Laboratory no. SO–A–292). Spikelets were softened by treatment with a few drops of this solution for a few minutes and kept moist by drops of water during dissection.

For studies of starch the single mature caryopsis available was soaked in a mixture of equal parts Aerosol OT Solution and water for one and a half hours. Cross-sections were made by hand, cutting with a razor blade the material positioned between two pieces of pith. The sections were stained with a drop of IKI for about 20 seconds, washed in water, and mounted in glycerine.

Anatomical observations were made with the Leitz Ortholux microscope, equipped with plano objectives, and photomicrographs were taken using this microscope and Kodak Panatomic-X film (ASA 32). Bright field, phase contrast, polarized light, and dark field were used. Dissections were studied under the Wild M 5 Stereo-microscope and drawings were made with the aid of the Wild drawing tube. Anatomical drawings were made using the Wild M 20 microscope, also with the aid of a Wild drawing tube. Illustrations of the habit of the plant were made from herbarium specimens and field photographs.

Voucher specimens of the plants reported in this paper are filed in the United States National Herbarium, Smithsonian Institution. The collection of material in liquid preservative is also maintained at the same location.

Maclurolyra tecta, new genus and species

Figures 4–7

Description.—*Gramen* perenne sylvarum umbrosarum, usque ad 48 cm altum. *Culmi* erecti, sine ramis, plerumque 20–48, cm alti, nodis 4–6, foliis 1–3. *Foliorum vaginae* cum setis ca. 1.5 mm longis e marginibus superioribus emanentibus;

FIGURE 4.—Habit sketch of *Maclurolyra tecta*: *a*, Habit of the plant, × ½; *b*, mature inflorescence in its position behind the blade, × 1. Based on *Calderón* 2084.

ligula ca. 0.5–1.2 mm longa, ciliata; petiolus ca. 4–7 mm longus, 180° tortus; laminae asymmetricae, plerumque 10–21 cm longae, 3–5 cm latae, oblongo-lanceolatae, glabrae, venatione tessellata. *Inflorescentia* rigida, symmetrica, anguste fusiformis, solitaria et in culmo terminalis, 2.7–7 cm longa; spiculae unisexuales, 1–florae, approximatae. *Spicula feminea* fusiformis, 9.5–11.5 mm longis; glumae subaequales, lanceolatae-acutae, glabrae, coriaceae, apice leviter curvatae et cucullatae; gluma inferior 9–11.5 mm longa, 5–6 nervata; gluma superior 9.5–11 mm longa, 5–7–nervata; lemma 9.7–11 mm longum, depressum, anguste lanceolatum, acuminatum, coriaceum, maturitate crustaceum, pilis longis appressis vestitum; palea 8.5–9.5 mm longa, in textura lemma simulans, villosa, ecarinata, 2–nervata; lodiculae 3, nervatae, 0.7–1 mm longae; staminodia 3, ca. 0.33 mm longa; ovarium fusiforme, stylo 1, longo, tereti, infra medium antrorso-hirsuto, stigmatibus 2; caryopsis hilo lineari, embryone basali, 1/8 longitudinis fructus aequanti. *Spicula masculina* lanceolata, subovoidea, 4–5.25 mm longa, pedicello gracili ca. 8 (4–9) mm longo, sine glumis, lemmate paleaque in facie et in textura glumas femineas simulantibus; lemma ca. 4–4.5 mm longum, glabrum apice scabrum, 8–10–nervatum; palea 4.4–5 mm longa, lemmate longior, ecarinata, nervis 4–6 fortibus; lodiculae 3, nervatae, 0.75–1.05 mm longae; staminodia 3, minuta; stamina 3, antheris 1–1.5 mm longis.

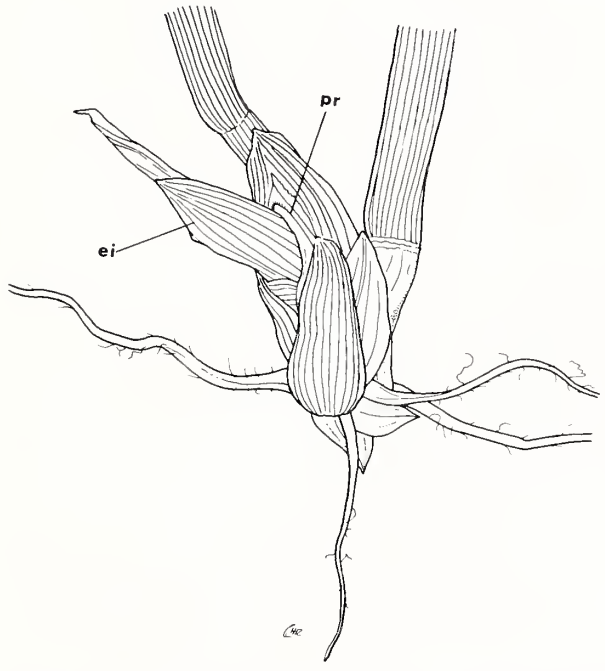


FIGURE 5.—Extravaginal innovation (*ei*) of *Maclurolyra tecta* with its prophyllum (*pr*), as shown breaking through a basal bract. Based on *Calderón* 2080, × 3.6.

Perennial grass in discrete caespitose clumps, usually crowded above and somewhat open below, spreading by very short, determinate rhizomes emerging from prophyllate buds at a subterranean node of the culm or at the base of young shoots, internodes of rhizome reduced or up to 1 cm long; lateral shoots intravaginal or, more frequently, extravaginal, each one producing a new bud in rapid succession, but axis at first strongly diageotropic, curved upward and giving rise to a culm; bud prophyllum ovoid-lanceolate, short-ciliate at the tip, 2–keeled, the keels winged; new aerial shoots extending upward ca. 21 (5–26) cm before unfolding of the leaves.

Culms unbranched, erect or geniculate-ascending, usually 20–48 cm tall; internodes solid, upon drying becoming softer toward the summit, sulcate-ridged, the lowermost glabrous, the succeeding ones with minute retrorsely appressed hairs in the furrows above the middle, almost glabrous below; internodes at the base and at the apex of the culms short, the intermediate ones (usually the 3rd) greatly elongated; nodes 4–6, usually more in the first shoots succeeding the seedling culm, covered by a dense, retrorse, white pubescence, the lower ones less pubescent than the upper ones, slightly prominent unless geniculate, narrow in the center, all gemmiferous; buds solitary above the locus of the sheath attachment; flowering culms with 1–3 fully developed leaf blades; culms succeeding the seedling developing more than 3 (up to 6) leaves, these culms rather small and weak, less than 20 cm tall.

Leaves exhibiting acropetally a progressive strong modification in size, shape, vestiture, and degree of blade development; leaves at base of the culm small, scaly, loose, broadly triangular-acute, glabrous, usually broken by root primordia, the succeeding ones consisting of the sheath with the blade obsolete or reduced to a minute mucro, much shorter than the internode, inflated, rounded on the back, glabrous, glossy and sulcate, violet; midculm sheaths shorter than the internode, inflated, glabrous or glabrescent above, the upper edge short-pilose to ciliate; blade very reduced or

up to 7 mm long in the successive leaves, lanceolate-acute, margins scabrous; uppermost 1–3 leaves with a completely developed blade. *Sheaths* imbricate, longer than the internode, moderately inflated and slightly keeled above, sulcate, glabrous on the back, with coarse white antrorse or retrorse minute bristles on the sides, ciliate along the outer margin, with long bristles (setae) ca. 1.5 mm on the distal edge on both sides of the petiole. *Ligule* ca. 0.5–1.2 mm long, somewhat thick, ochraceous, ciliate. *Petiole* ca. 4–7 mm long, twisted 180°, very thick in the middle (pulvinate), glabrous on the abaxial surface, densely hirsute on the adaxial surface, narrowly winged on the margins by the decurrent blade, strongly asymmetrically placed in relation to the sheath. *Blade* asymmetric, flat, rather stiff, erect or ascending to horizontal, mostly 10–21 cm long, 3–5 cm wide, oblong-lanceolate, acuminate above, terminating gradually in a sharp tip, asymmetrically rounded at the base, almost oblique on one side, glabrous on both surfaces, slightly glaucous on the abaxial surface, antrorse-scabrous on the margins from above the middle to the tip; midrib pale and prominent on both surfaces, primary nerves 4–7 on each side of the midrib, pale and manifest on the abaxial surface, less discernible on the adaxial surface; all nerves connected by transverse veinlets, these manifest to superficial view on the abaxial surface, somewhat obscured on the adaxial surface.

Inflorescence rigid, symmetric, narrowly fusiform, consisting of more or less densely aggregated groups of spikelets; inflorescence appearing solitary and terminal to the culm, ascending, slightly nodding, more often abruptly curved or bent laterally or downward; reproductive bud, related to the main flowering axis in its basal portion, developing into a very reduced, inconspicuous, lateral shoot, with an inflorescence ca. 1 mm long or more frequently remaining dormant, its subtending leaf (bract) lacking, but the prophyllum well developed, membranous, 2–keeled, ca. 8.5–14 mm long, enclosing the lateral shoot, basal internode of lateral shoot very reduced, 0.63–0.75 mm long; basal part of the main inflorescence axis with its lateral product covered for almost its whole length by the uppermost leaf sheath, the exserted portion 2.7–7 cm long, the unbranched part extending 0.2–1.5 cm beyond, terete, sulcate, densely hispid; rachis subtrigonous or angular by the initiation of branches, progressively more slender and almost glabrous above.

Spikelets unisexual, dimorphous and 1–flowered, closely appressed and uniformly mixed throughout the inflorescence; female spikelet subsessile, terminal to a very short lateral branch, the pedicel very short, thick, clavate, somewhat flattened and sulcate in young specimens, hispidulous below, glossy toward the cupulate apex; male spikelet long-pedicellate (usually one per female, just below it), the pedicel slender, sulcate, scabrous or short-hispid, straight or basally curved upward, ca. 8 (4–9) mm long; spikelets both deciduous by abscission below the glumes in the female or below the anthecium in the male, at maturity the female falling first and the male remaining longer in the inflorescence.

Female spikelet fusiform, slightly depressed, 9.5–11.5 mm long; glumes subequal, of the same length as, or a little shorter than, the anthecium, lanceolate-acute, rigid, coriaceous, increasingly indurate toward the slightly curved and cucullate apex, smooth, glabrous, short-hispid on the tip; lower glume 9–11.5 mm long, 5–6–nerved, upper glume 9.5–11 mm long, 5–7–nerved, the nerves prominent, extending to the apex, the median one

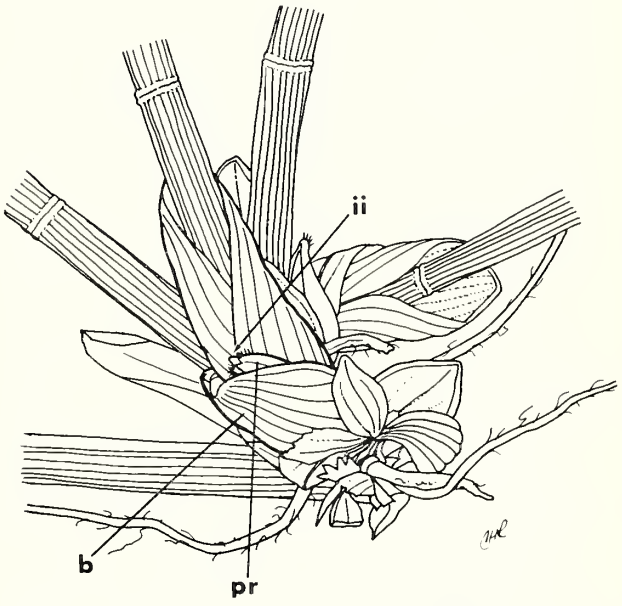
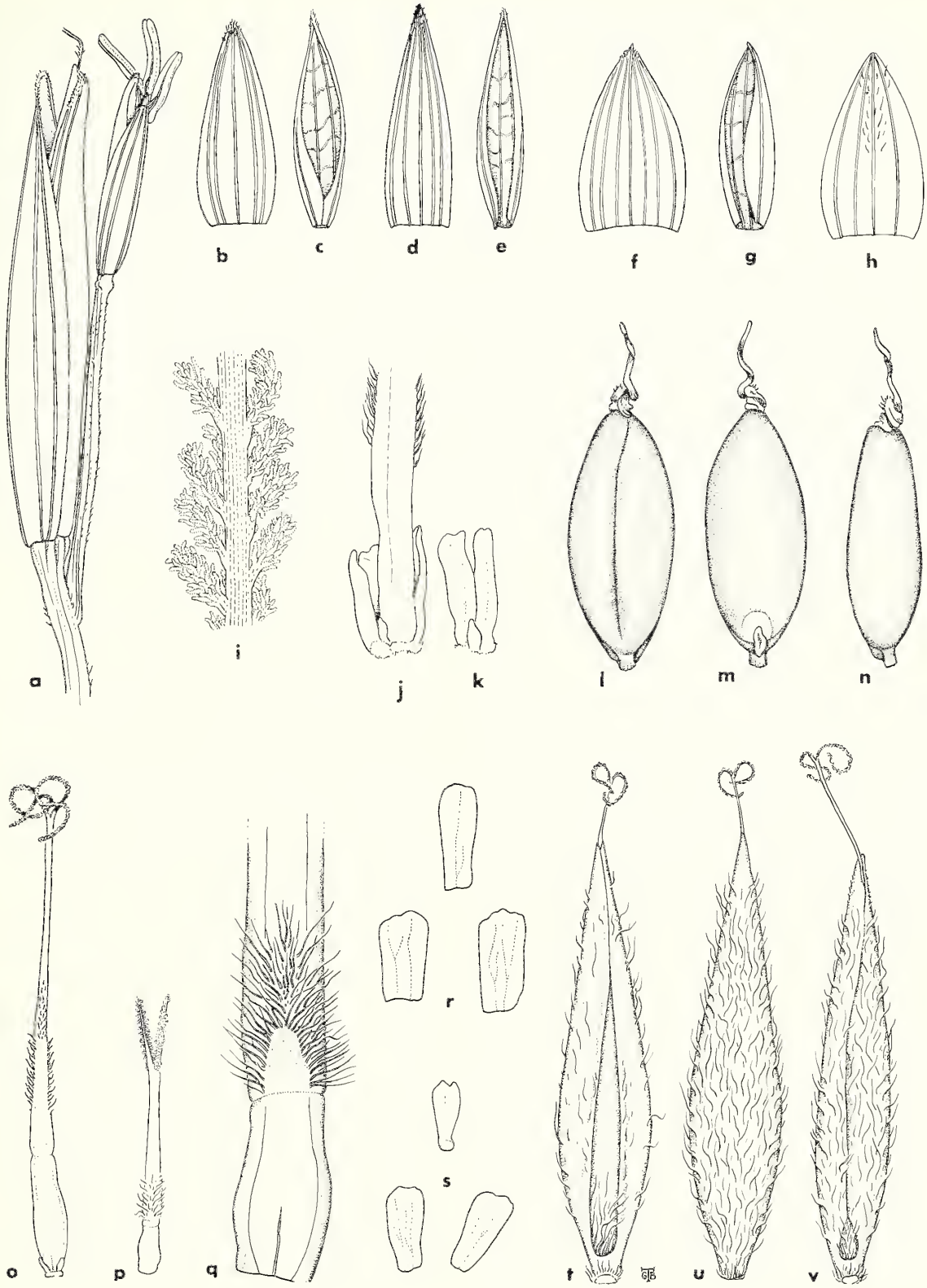


FIGURE 6.—Intravaginal innovation (*ii*) of *Maclurolyra tecta*, still within its prophyllum (*pr*) and growing directly upward from within the bract (b), × 3.6. Based on *Calderón* 2084.

quite separate from the lateral ones, connected by transverse veinlets, these more noticeable from the inside; margins of the glumes inflexed along the outer nerves, those of the lower glume embracing the upper glume, upper glume lobate at the base, embracing the anthecium. Lemma 9.7–11 mm long, depressed, narrowly lanceolate, acuminate, margins slightly separated below, overlapping and completely covering the palea, strongly convolute at the indurate apex, coriaceous, increasingly firm, crustaceous at maturity, entirely covered by long, appressed hairs; nerves weakly manifest on the abaxial surface at maturity, usually 7 (5–8). Callus very short, ca. 0.25–0.3 mm long with a rim of hairs at the base. Palea 8.5–9.5 mm long, of the same texture as the lemma, villous throughout, compressed on back, not keeled, 2–4–nerved (the nerves obscure), elliptic-acuminate, convolute, with a hard inrolled tip, tightly enclosing the flower. Axis of the spikelet developed into a short rachilla segment between the lemma and the palea, ca. 0.5–0.75 mm long. Lodicules 3 (rarely 4), usually 0.7–1 mm long, one median and posterior, the other two lateral and anterior, arranged in one whorl, the posterior lodicule not attached to the palea, rectangular or oblong-elongate, obliquely truncate, irregular or a little lobed at the tip, moderately thick throughout with a well developed vascular system originating from one vascular strand which, immediately after entering the base of the lodicule, produces 3–5 traces extending to about three-fourths of the length of the lodicule and connected by lateral branches, the posterior lodicule narrower, sometimes a little shorter. Staminodes 3, in one whorl at the base of the ovary and alternating with the lodicules, small, ca. 0.33 mm long, bractlike, triangular-obtuse, sometimes very reduced and not vascularized. Gynoecium: Ovary fusiform, slightly depressed, glabrous, attenuate at its apex; style one, long, terete, slender above, a little flat, broad and antrorse-hirsute below the middle, the hairy zone up to 2.5 mm long, and ca. 1.75 (1.3–1.9) mm above the ovary apex; stigmas 2, obtuse, short, and erect when young, long and spiraloid at maturity, the adaxial surface covered with globose stigmatic proliferations aggregated into short branches, the distal portion of the style and stigma long-exserted through a very small apical opening of the anthecium. Caryopsis tightly enclosed by the lemma and palea, free inside, chestnut-colored, glabrous, 5.5 mm long and 1.8–2.0 mm broad, oblong-oval, ventrally flattened, slightly convex on the dorsal side, not sulcate with a rather long, basally coiled style, persistent at the apex; hilum linear, extending the whole length of the caryopsis; embryo basal, small, about one-eighth of the total length of the caryopsis; starch grains compound.

Male spikelet smaller than the female, lanceolate, subovoidal, depressed, 4–5.25 mm long. Glumes not developed or rarely reduced ones present, the lemma and palea resembling in appearance and in texture that of the glumes of the female spikelets. Lemma broad-lanceolate, acute, slightly clasping the palea at the base, ca. 4–4.5 (3.5–5) mm long, rigid, moderately indurated, glabrous with the tip scabrous or minutely pilose; strongly 7 (8–10)–nerved, the nerves extending to the apex, 3 or 5 of them fused at the apex and forming a slightly cucullate tip, incurved toward the palea. Callus ca. 0.3–0.5 mm long, developed between the lemma and the palea and covered by the base of the lemma. Palea lanceolate-fusiform, subacuminate, 4.4–5 mm long, exceeding the lemma and of the same texture as it, with 4–6 strong nerves extending to the apex, not keeled, compressed or slightly convex on the back, with the margins overlapping, enclosing the flower. Lodicules 3, in one verticil, similar to those of the female flower, but a little smaller and thinner, ca. 0.75–1.05 mm long, vascular traces 3–6, the posterior lodicule usually smaller and with 1 vascular trace. Staminodes 3, minute, scaly, occasionally developed as a filament-

FIGURE 7.—*Maclurolyra tecta*, spikelet details: *a*, Partial inflorescence consisting of the female and male spikelets, × 6. Glumes of female spikelet, × 3: *b*, upper glume (external view), *c*, upper glume (internal view), *d*, lower glume (external view), *e*, lower glume (internal view). Lemma of male spikelet, × 6: *f*, external view, *g*, internal view. *h*, Palea of male spikelet, × 6; *i*, portion of stigma, greatly enlarged; *j*, base of gynoecium with lodicule and staminode, × 12.5; *k*, lodicules with staminode at the base, × 12.5. Caryopsis, × 6: *l*, hilum side, *m*, embryo side, *n*, lateral view. *o*, Completely developed gynoecium with staminodes at the base, × 6; *p*, young gynoecium, × 6; *q*, base of young gynoecium showing details of hairy zone, × 25; *r*, lodicule complement of female spikelet, × 12.5; *s*, lodicule complement of male spikelet, × 12.5. Anthoecium, × 6: *t*, front view showing palea exposed, *u*, back view, *v*, front view showing lemma enveloping the palea and style exserted apically. All drawings based on *Calderón* 2084.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ous appendage placed between the lodicules and stamens and alternating with them. Androecium: Stamens 3, anthers oblong, 1–1.5 mm long, filaments elongated at anthesis, exserted at the apex through a minute opening between the lemma and palea. Gynoecium often present, rudimentary to somewhat developed, bearing an ovule and 2 or 3 stigmas.

Material Examined.—*Type:* Panama: Provincia de Colón: Santa Rita, ca. 25 km before Colón on the Carretera Transístmica (Transisthmian Highway). End of the timber road. Abundant in the woods, especially in the ravine and near the stream. Inflorescences hidden beneath the leaves; some rise above them but remain covered by the torsion of the axis of the inflorescence and that of the leaf petiole. Leaves thick, hard, and rigid. Blade divergent or horizontal. 9 March 1968, *Cleofé E. Calderón* 2084 (Holotype: US; Isotypes: BAA, F, K, MO, NY, P).

Additional Collections: Panama: Provincia de Colón: Santa Rita, ca. 25 km before Colón on the Carretera Transístmica, timber road. 5 March 1968, *Cleofé E. Calderón* 2080 (BAA, F, K, MO, NY, P, US). Santa Rita: ca. 10 km east of the Carretera Transístmica by timber road, alt. 300 m, ca. 79°45′W longitude, 9°21′N latitude, 2 October 1971, *C. E. Calderón and R. L. Dressler* 2130 (BAA, F, K, MO, NY, P, US), *C. E. Calderón and R. L. Dressler* 2132 (seedlings, US). Provincia de Panamá: Cerro Jefe, alt. ca. 900 m, 8 March 1968, *C. E. Calderón* 2082 (US). "La Eneida," 5 km NE of Cerro Jefe, alt. 800 m, 29 October 1971, *C. E. Calderón and R. L. Dressler* 2138 (BAA, F, K, MO, NY, P, US).

Seedling

Seedlings of *Maclurolyra* were found in all stages of development around the periphery of the parent plants in the forests of Santa Rita, Panama, in October of 1971. The parent clumps were still blooming vigorously, so that flowering and development of seedlings occur simultaneously. The seeds doubtless germinate very soon after they fall to the ground. In the olyroid grass, *Cryptochloa,* we have even found seeds germinating while still attached to the inflorescence.

Differences in grass seedlings and their taxonomic value were observed by Avdulov (1931), who recognized two types based on the shape and position of the first seedling leaf. In his Type I ("panicoid grasses"), the first seedling leaf is broad, oval or lanceolate, and horizontal or ascending in position, while in his Type II ("festucoid grasses"), the first seedling leaf is long and narrow, and more or less vertical in position.

More recently Kuwabara (1961a) presented a classification of grass seedlings in which he recognized three types, based on the position of the first seedling leaf. These are (1) perpendicular type, (2) ascendant type, and (3) horizontal type. The first type is found in festucoid grasses, while the second is found in eragrostoid and some panicoid grasses, and the third type is found in other panicoid grasses.

We have observed the seedlings of a few other species of olyroid grasses—*Lithachne pauciflora, Olyra loretensis, Piresia sympodica*—and a species of the related genus *Pariana,* and found them all to be similar to that of *Maclurolyra.* These seedlings cannot be assigned to any of the types defined in the literature.

Although a "bambusoid type" of seedling has not been defined, seedlings of various genera of bamboos have been illustrated, and the seedlings of *Maclurolyra* and the bambusoid grasses mentioned above, are of the same type. Some drawings and short descriptions of bamboo seedlings are found in Arber (1934), Jacques-Félix (1962), and McClure (1966). To our knowledge one of the most complete descriptions and illustrations of bamboo seedlings is that given by Velenovský (1914) for *Bambusa arundinacea* and *Schizostachyum acutiflorum.*

We may, therefore, define the "bambusoid type" of grass seedling as follows: coleoptile short and not elevated from the caryopsis by an internode, first two to several leaves bladeless or with a reduced blade, first expanded blade broad, ovate-lanceolate, horizontal in position.

The fact that the coleoptile (Figure 9[*co*]) in the seedling of *Maclurolyra* is not elevated above the lemma suggests that no internode was present in the embryo where the vascular traces diverged to the scutellum and to the plumule, one of the features of the bambusoid type of embryo as defined by Reeder (1962). This is unlike the situation found in panicoid grasses, for example, where such an internode exists and elongates upon

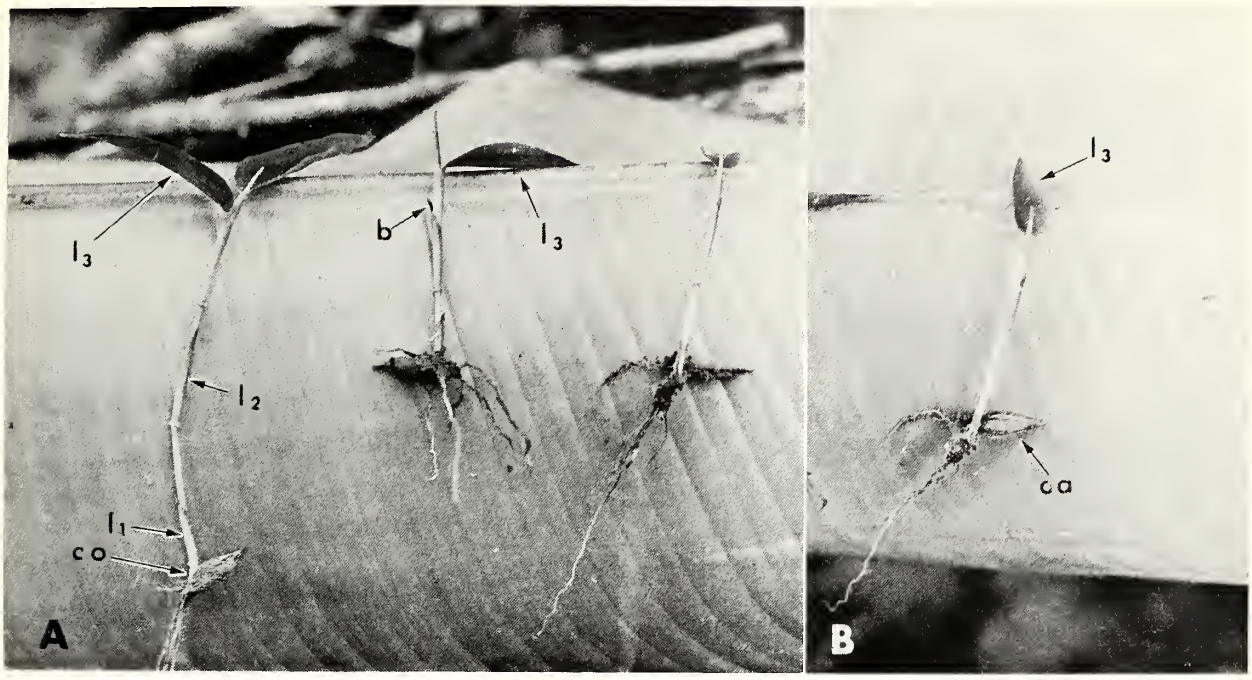

FIGURE 8.—*Maclurolyra tecta* seedlings in the field (Santa Rita, Panama): A, three seedlings in different positions; B, single seedling arranged to show shape of first developed blade. [*b*=blade, *ca*=caryopsis, *co*=coleoptile, l_1=first leaf, l_2=second leaf, l_3=third leaf (with a completely developed blade).] Seedlings are part of *Calderón* 2132.

germination, elevating the coleoptile above the caryopsis.

The seedling of *Maclurolyra* (Figures 8, 9) has at its base a 2–nerved coleoptile, which is the first structure to have broken through the caryopsis upon germination. While still in the embryo it was a sheathing structure that covered and protected the plumule, but is shown here ruptured, a condition which came about when the new shoot elongated and broke through it. The position of the coleoptile is next to the lemma at the point where it emerged.

The first and second leaves of the primary shoot consist of a sheath and a very reduced ovate blade with no separation between the two. The third leaf consists of a sheath, a short petiole, and a blade—the first expanded blade of the new plant. This blade is ovate-lanceolate, symmetrical, 14–18 mm long, 6–7.5 mm wide, and horizontal in position. There is a rapid elongation of the first internodes, which surpass their sheaths in length and leave the nodes exposed. The fourth leaf develops soon after the first, has conduplicate vernation, and the blade of this leaf, as all others that follow it, is asymmetrical.

Seedlings of oryzoid grasses exhibit some similarity to bambusoid seedlings in the presence of leaves with reduced blades prior to the first one with a developed blade. However, the first developed blade is linear rather than ovate-lanceolate and assumes an ascending rather than horizontal position. Kuwabara (1961b) described and illustrated seedlings of two oryzoid grasses—*Leersia oryzoides* and *Zizania latifolia*—but did not assign them to any of his three types.

The term "first seedling leaf" as previously used in grass systematics should now be understood to mean "first seedling leaf with an expanded blade." The reason for this becomes apparent when we consider the bambusoid or oryzoid seedling in which the actual first seedling leaf consists only of a sheath or a sheath with a reduced blade. It is the seedling leaf that bears the first expanded blade that has taxonomic value, and in these groups this blade occurs on one of the leaves following the first.

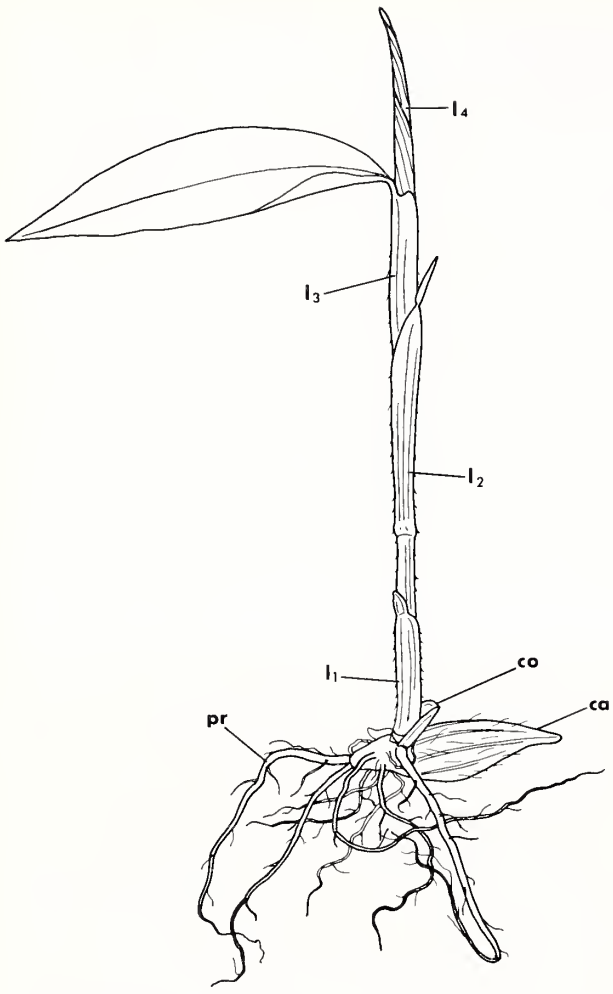

FIGURE 9.—Seedling of *Maclurolyra tecta*, × 3. [*ca*=caryopsis, *co*=coleoptile, l_1=first leaf, l_2=second leaf, l_3=third leaf (with blade); l_4=fourth leaf, still unfolded; *pr*=primary root.]

Torsion of the Leaf and Inflorescence

At anthesis, the inflorescences of *Maclurolyra* are usually found behind the subtending leaf blade (Figures 3*d,f*, 4) while most of the young ones are in front of it (Figure 3*a,b,e*). This comes about by a twisting of the petiole (Figure 3*d*) of the subtending leaf and also the axis of the inflorescence (Figure 3*c*). The twisting exhibited by the petiole shows that the leaf blade turns around the inflorescence along a vertical axis changing its position. The axis of the inflorescence also moves around at the same time until it is covered by the leaf blade. After maturity, the inflorescence bends downward (Figure 3*e,f*) and assumes a position of almost right angles to the culm.

In the seedling the petioles of the first leaves are not twisted (Figures 8*a*, 9). In the first few culms which develop from the seedling and have three or four leaves, the uppermost leaf that subtends the inflorescence exhibits a strong twisting of the petiole, while in those below, the twisting is less evident, and in the lowermost leaf the petiole is usually not twisted. This seems to indicate that torsion of the petiole is a phenomenon related to the relative position of the blade and inflorescence.

The position of the inflorescence and the subtending leaf, with the latter covering the former, suggests that the leaf has a protective function. The blade covers the inflorescence at the time of anthesis when the stamens and stigmas are exposed and perhaps protects the flowers against an excess of rain. We have noticed that such a situation occurs in other members of the Olyreae where the inflorescences are hidden under the leaves, as in *Diandrolyra bicolor, Raddia costaricensis,* and some species of *Cryptochloa.*

Leaf torsion was the subject of discussion in broad-leaved grasses by Arber (1934:289). Petiole torsion has been described in the distantly related genus *Pharus* by Lindman (1899) and Kugler (1928), but in the case of this genus torsion takes place along a horizontal axis and reverses the morphologically lower and upper surfaces of the blade. In *Maclurolyra,* torsion of the petiole occurs along a vertical axis so that the morphologically lower and upper surfaces of the blade are not really reversed since it is always in an ascending position as it moves around the inflorescence.

Leaf movement in another olyroid grass was described much earlier by Brongniart (1860) who spoke of "sleep movements" in *Raddia guianensis* [= *Strephium guianense*]. We have also observed this phenomenon in plants of *Lithachne pauciflora* where the blades, horizontally held during the day, become reflexed at night. This diurnal movement occurs at the base of the petiole where the pulvinus is located. In many herbaceous bambusoid grasses and in bamboos where the leaf complement consists of a number of overlapping sheaths, the petiole of each leaf is twisted slightly to allow all blades to lie in the same plane, a point commented upon by Holttum (1958:13).

Leaf torsion appears to be a common phenomenon in the Bambusoideae, although its *raison d'être* is not the same in all cases. In many cases its function is to bring all leaves of a leaf complement into a single plane, in others it is diurnal in character, and in others—as in *Maclurolyra*—it represents a more permanent twisting which brings the subtending leaf of the inflorescence into a position of protection.

Observations of living plants of *Macurolyra* over longer periods of time will be needed to understand more thoroughly what kinds of movements are involved and their biological significance. Concerning this subject we fully agree with Arber (1934:292) who remarks, "The problem of the extent to which torsion and resupination are autonomous movements, and of the degree to which they are influenced by external conditions, such as light and gravity, has not been solved with any completeness. It is a direction in which further work is needed . . . ."

Morphology of the Inflorescence

As is well known, the floral structure of a grass consists of one or more flowers inclosed in bracts which form a discrete aggregation known as the spikelet. For descriptive purposes the spikelet is considered to be the unit of the inflorescence. Spikelets are arranged in various ways in different grasses, the most common arrangements being the spike, raceme, and panicle. These terms, however, are borrowed from the descriptive vocabulary of other flowering plants in which they refer to the arrangement of individual flowers in an inflorescence.

In recent years, the study of inflorescence morphology has received greatest attention from W. Troll and his students, and there exists a voluminous literature on this subject. The correct interpretation of the inflorescence, difficult at best in other flowering plants, is all the more so in grasses where the individual unit is the spikelet rather than the flower. This is all the more complicated by the fact that the morphological interpretation of the spikelet itself is beset by conflicting theories, for example whether the ultimate production (gynoecium and ovule) is cauline or foliar in origin.

In the inflorescences of many flowering plants the presence of subtending leaves and prophylla facilitates the analysis of the inflorescence type. The inflorescences of the majority of grasses, however, lack these subtending leaves and prophylla. Within genera of bambusoid grasses many patterns of inflorescence exist, some of them complicated systems of ramification, but often with bracts and prophylla developed.

Probably one of the first attempts to describe in detail the arrangement of a bamboo inflorescence was that made on *Schizostachyum* by McClure (1934). The subject has also received attention from Holttum (1956, 1958), and, more recently, an interpretation of a bamboo inflorescence (*Melocanna bambusoides*), based on morphological analysis, was made by Petrova (1965). In 1970 the same author reported on the inflorescence morphology of species of the bamboo genera *Phyllostachys, Pseudosasa,* and *Sasa.*

We have attempted to interpret the inflorescence of *Maclurolyra* and some of its allies according to the system of Troll, as basically presented in his treatise of 1964. We are especially grateful to him for the assistance he gave in the interpretation of the inflorescences of the olyroid group of grasses which he and H. Weber examined during Calderón's visit to their laboratory in Mainz.

Because of the great diversity of inflorescence patterns encountered in genera of the Bambusoideae and their systematic value, we feel that it is extremely important that particular attention be paid to them. In the following descriptions of the inflorescences of *Maclurolyra* and related genera, we are employing the terminology of Troll (1950, 1958, 1964). Because these terms have not yet been commonly applied to grasses, we feel that the following definitions of these terms, as we apply them to the Olyreae, will be useful in understanding the discussion which follows. In order to avoid confusion and allow the reader to make comparisons with the published inflorescence schemes of Troll, we are retaining the German abbreviations both in our descriptions and schemes. The original German terms and their abbreviations appear in parentheses in the following definitions.

Partial Inflorescence (PJ, *Partialinfloreszenz*): A series of flowers (or spikelets) terminating the main shoot and the successive secondary floral axes produced by the first. These partial inflorescences are the so-called panicles or racemes in the tradi-

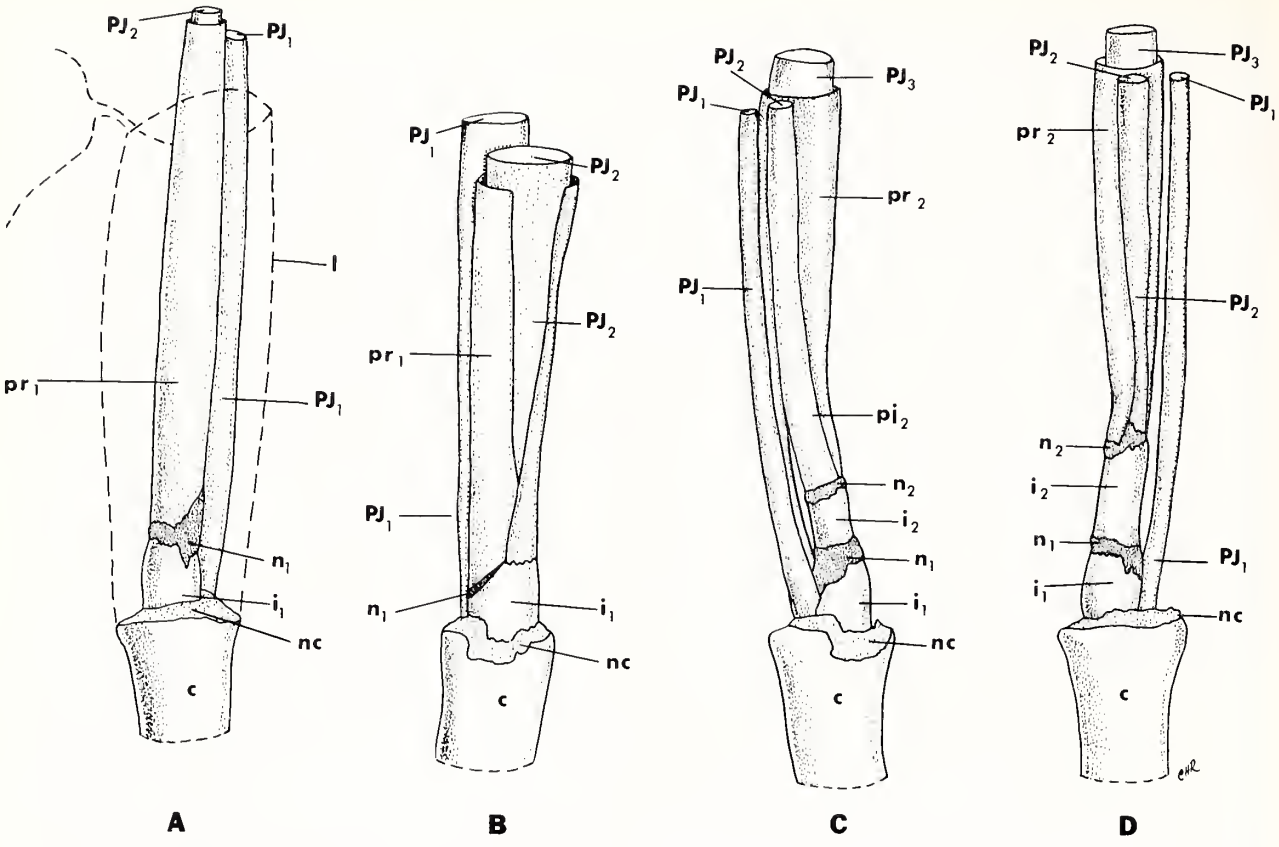

FIGURE 10.—Schematic of a dissection of a synflorescence of *Olyra latifolia*: A, front and B, lateral views of the base of the synflorescence after removal of the uppermost leaf of the main culm; C, front and D, lateral views of the same synflorescence with the first prophyllum removed. [c=main culm, i_1=first internode; i_2=second internode, l=uppermost leaf of the main culm, n_1=first node; n_2=second node, nc=node of the main culm, PJ_1=first partial inflorescence, PJ_2=second partial inflorescence, PJ_3=third partial inflorescence; pr_1=first prophyllum, pr_2=second prophyllum.]

tional systematic descriptions of the floral systems of the Olyreae.

COMPLEX INFLORESCENCE (*Komplexe Infloreszenz*): A general descriptive term which refers to any type of compound inflorescence, but which implies no morphological connotation.

BRACT (b, *Brakt*): The subtending leaf (H, *Hochblatt*) in the axil of which a floral bud or floral shoot is found. This bract may be a reduced foliar appendage or may have the appearance of a normal leaf with a sheath and a developed blade (L, *Laubblatt*).

PROPHYLLUM (vb, *Vorblatt*): The first foliar organ of a lateral shoot, usually bikeeled.

FLORESCENCE (*Floreszenz*): The series or group of flowers at the end of a shoot. In the typology of the synflorescence of Troll, florescence is the equivalent of the descriptive term "partial inflorescence."

MAIN OR PRIMARY FLORESCENCE (HF, *Hauptfloreszenz*): The group of flowers, or florescence, found at the end of the main shoot.

COFLORESCENCE (CF, *Cofloreszenz*): Any lateral florescence below the main one.

PARACLADIUM (Pc, *Parakladium*): The shoot (s) arising from the main axis immediately below the basal internode of the main florescence, at the end of which the coflorescence (s) is found. The paracladia repeat the structure of the main axis.

SYNFLORESCENCE (*Synfloreszenz*): The whole floral aggregation in a plant, i.e., the system of the main florescence with its coflorescences.

SUPPLEMENTING ZONE (BZ, *Bereicherungszone*): That part of the main shoot, below the main flores-

cence, in which paracladia are produced, thereby supplementing or enriching the flowering system of the plant.

Inhibition Zone (HZ, *Hemmungszone*): The purely vegetative part of the main shoot below the synflorescence in which the buds do not develop under normal circumstances.

Innovation Zone (JZ, *Innovationszone*): That part of the axis in which buds give rise to new aerial shoots (innovations).

We shall first discuss the main system of ramification of the flowering system. In most of the Olyreae several inflorescences are borne in succession from a node either terminal to the main culm or terminal to a branch. This assemblage of inflorescences has the appearance of a single raceme or panicle since the individual inflorescences emerge close together, the lower part of their axes tightly appressed within the uppermost sheath of the culm in which they are inclosed.

In *Olyra latifolia,* as in many other species of this genus, the occurrence of spikelets is restricted to the uppermost nodes of the main culm and lateral branches when these are produced. The growth of the main culm and of the lateral branches is limited by the production of spikelets. The distal node of the culm or of a vegetative branch produces a leaf, usually with a completely developed blade. The meristematic shoot apex rapidly continues its growth and develops a terminal inflorescence, in the case of *Olyra latifolia* with the appearance of a "panicle." This first floral production is in fact the first partial inflorescence of a series of two to several. From the distal node of the culm, and at the base of the primary or main inflorescence, a second one is borne (Figures 10*a, b,* 11*b*). This second partial inflorescence develops from a lateral floral bud in the axil of the uppermost leaf. The lateral floral branch has a very well-developed prophyllum, which is addorsed to the axis of the primary inflorescence, is two-keeled, and incloses the newly developing inflorescence. Shortly afterwards this floral bud develops a second inflorescence (Figures 10*c, d,* 11*b*), the initiation of a third one taking place at the base of this secondary axis. The third inflorescence, like the second one, is inclosed within a prophyllum which completely envelops it, but no trace of a bract is found at its base. The succeeding partial inflorescences continue to develop in the same fashion. A shortening of the basal internode occurs in *Olyra latifolia* and in the several species of the Olyreae that we have studied so far. In each partial inflorescence the distal internode, or epipodium, is quite elongated.

The main features of the type of inflorescence system found in *Olyra* can be summarized as follows: The production of lateral floral branches is limited to one. Each partial inflorescence, commencing with the main or first one, produces only one lateral floral axis. The second floral axis also produces only one lateral axis, and so on. Thus the first branching system of the total inflorescence is monochasial, representing a complex inflorescence of the cymose type. The partial inflorescences of the first order are also complex inflorescences in themselves but of a different type. It is outside the scope of this paper, however, to present a detailed analysis of the partial inflorescence of *Olyra latifolia.* We can, nevertheless, refer to the partial inflorescence as a *paniculodium,* according to Troll (1967:94, 1968:105).

We feel that the term synflorescence (Troll, 1950: 383, 1964) should be used to designate the total series of inflorescences. Partial inflorescences of the first order are the individual floral axes where the spikelets take the place of single flowers. A more precise terminology could be used, but according to Troll (1964) only in a typological analysis based on homologies.

In *Bulbulus,* another genus of Olyreae, the bracts or subtending leaves are present and consist of a sheath and a small blade. In this genus the main culm terminates in an inflorescence, the axis of which exhibits a structure much more complicated than that of *Olyra* (Figure 11*c*). At the basal node of the main floral axis is found a bract in the axil of which occurs a bud, inclosed in its prophyllum. This bud does not develop into a lateral floral branch as in the example described above. Distal to this node, on the same lateral axis, and separated by a fairly long internode, is found another node which bears a bract. This bract, like the other ones found at the base of the first partial inflorescence, consists of a completely developed sheath and reduced blade. The second partial inflorescence emerges from the axil of this second bract. At the base of this second partial inflorescence there is also a prophyllate bud which remains dormant but no bract is found. The lateral branch elongates into an

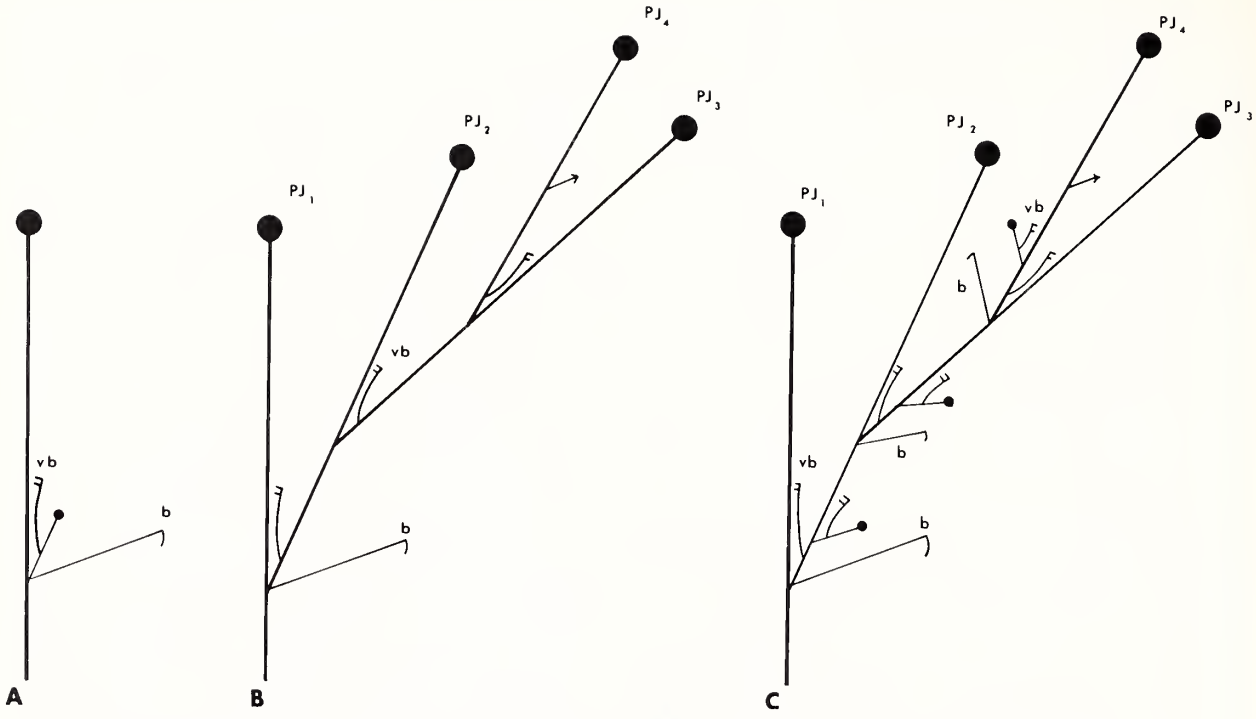

FIGURE 11.—Schematic of the synflorescences of A, *Maclurolyra tecta*; B, *Olyra latifolia;* and C, *Bulbulus nervatus*. [*b*=bract, *PJ*=partial inflorescences of successive orders (1–4), *vb*=prophyllum.]

internode and the next node repeats the same construction. The production of partial inflorescences in *Bulbulus* is not so prolific as it is in *Olyra latifolia*. Usually it forms only three or four partial inflorescences of the first order.

If we now turn to *Maclurolyra* we encounter a pattern of inflorescence somewhat similar to that of *Olyra latifolia* but one which is much simpler (Figure 11*a*). Both differ apparently in the construction of the partial inflorescence itself, i.e., in the arrangement of the spikelets. In *Maclurolyra* the synflorescence is terminal to the main culm. At the base of the main floral axis a bud within its prophyllum is found. In some specimens we have found only a rudimentary inflorescence about 1 mm long. The prophyllum is well developed but no bract is found; the proximal internode is also very short and the distal internode very long.

In *Olyra latifolia, Bulbulus, Maclurolyra,* and in most of the Olyreae, the axis of every partial inflorescence of the first order consists of a very short basal internode and a long distal internode, separated by a node. This is the first node of the lateral branch and the one that bears the prophyllum. The absence of bracts and the presence of well-developed prophylla seem to be general features of most of the genera and species of the tribe.

The first-order ramification of the synflorescence of *Olyra latifolia* is moderately simple. That of *Bulbulus,* on the other hand, is more complex, although its pattern still corresponds to that of *Olyra*. A less complex system is found in *Maclurolyra* where only one partial inflorescence, the main one, develops without further ramification.

The main culm of *Maclurolyra* does not produce lateral vegetative branches, whereas in *Olyra latifolia* such production is very frequent. In these cases, the pattern of ramification of the synflorescence appears to be like that of the branching at a node of the main culm, a feature which was observed in the genus *Bambusa* by Holttum (1958: 17–18).

Turning now to the structure of the partial inflorescence of first order, some similarities between those of *Maclurolyra* and *Bulbulus* are encountered. The female spikelet in *Maclurolyra* is subsessile

and the male spikelet is long-pedicellate, the latter sometimes overtopping the female. It is the female spikelet, however, which terminates the reduced lateral branch, with the male spikelets borne in a position below it. Usually only one male spikelet is found at the base of the female, i.e., in a monochasial fashion. The main axis of the inflorescence terminates in a female spikelet whose presence is sometimes obscured by several (4-6) male spikelets. This same situation also occurs in the partial inflorescences of *Bulbulus,* but these are more reduced and consist of only two or three pairs of spikelets.

In the typology of the inflorescence, Troll (1964) recognizes two basic types, the polytelic and the monotelic. In the polytelic type of inflorescence, a multiflowered florescence is found at the apex of the main floral axis. At the end of each lateral branch below the main florescence a similar florescence, designated as a coflorescence, is found. On the contrary, in the monotelic type, a single flower (E, *Terminalblüte*) is found at the apex of the main and lateral axes.

Troll (1965:130, 1968:105) states that the Gramineae, like the majority of the monocotyledons, have a polytelic type of inflorescence. According to his interpretation, the individual spikelets are referred to as florescences. The terminal spikelet of the total inflorescence, because of its special position, corresponds to the main florescence. The remaining spikelets, at the ends of lateral branches, are considered as coflorescences.

The polytelic condition refers basically to the spikelet structure, especially to that of the multiflowered ones in which the distichous arrangement of the floral members is continued by an extension of the spikelet axis, the rachilla, or a reduced floret. When the spikelets are uniflowered and there is no extension of the spikelet axis, the interpretation is more difficult. It has been suggested by Barnard (1957) that the flower in the Gramineae may be regarded as a branch system in which its parts differ in origin, some being cauline and others foliar. The origin of the ultimate floral production, the gynoecium and the ovule, is the subject of numerous controversial hypotheses and involves the interpretation of the whole spikelet structure.

In considering the type of inflorescence in grasses, the common usage of the term does not refer to the disposition of flowers on the floral axis but rather to the arrangement of the spikelets In the case of the Olyreae the spikelets are one-flowered and we have never observed a reduced second flower or prolongation of the rachilla.

In an attempt to describe very briefly the inflorescence of *Maclurolyra,* according to Troll's typology, the spikelet is treated here as comparable to a flower.

Figure 12 is a schematic representation of an entire plant of *Maclurolyra tecta.* The plant may be divided into three zones: (1) an innovation zone (JZ) from which the new shoots are produced from the base of the main culm and the nodes of the rhizome; (2) an inhibition zone (HZ), representing the vegetative zone of the main shoot where the axillary buds (which are found at every node) do not produce new paracladia; and (3) a supplementing zone (BZ) which refers to the part of the main shoot from which the paracladia (Pc) arise. The total system of florescences, or synflorescence, is formed by a "main florescence" (HF) and several coflorescences (CF) below. The main florescence is composed of a single female spikelet—which occupies the uppermost position—and 4-6 male spikelets below it. Below the basal internode (GJ:*Grundinternodium*) of the main florescence several paracladia arise, each one repeating the structure of the main florescence, but at a reduced grade. The paracladium of each coflorescence is extremely short and, as in the main florescence, bears a female spikelet in its upper part. Just below the female spikelet is found only one male spikelet.

The main axis of the synflorescence in *Maclurolyra* terminates in a spikelet as do each of the paracladia. In the analysis of the grass inflorescence, which is based on the spikelet instead of the flower, the inflorescence of *Maclurolyra* would be termed monotelic. If a typological analysis were made of the spikelet itself, the same conclusion would be reached, for the spikelet of *Maclurolyra* contains but a single flower which terminates the axis and beyond which there is no rachilla extension nor further production of flowers.

Troll (1968), however, considers the grass inflorescence to be polytelic, which is the condition found in the majority of monocotyledons. This is based on the fact that the multiflowered spikelet has the potential for further floral development, as shown by terminal rudimentary flower (s) or an extension of the rachilla. The uniflowered spikelet has been considered to be derived from the multiflowered

spikelet by reduction, as clearly seen in the case of *Calamagrostis,* for example, where the axis (rachilla) extends beyond the single floret.

We might therefore ask whether the synflorescence of *Maclurolyra,* along with that of other members of the Olyreae, is indeed monotelic, or if it represents a form of the polytelic type. Troll (1968:105) has recorded exceptions to polytely in other monocotyledonous families, such as the Scheuchzeriaceae, Juncaginaceae, Alismataceae, and Burmanniaceae. Weberling (1965:220) has pointed out that when exceptions occur in a polytelic family, the more primitive genera exhibit a monotelic type of synflorescence. Among the dicotyledons, for example, *Sambucus* and *Viburnum* have monotelic inflorescences while those of the more advanced genera of the same family (Caprifoliaceae) are polytelic. If exceptions to polytely do occur in the grass family, we should perhaps not be surprised to find them in the less advanced genera.

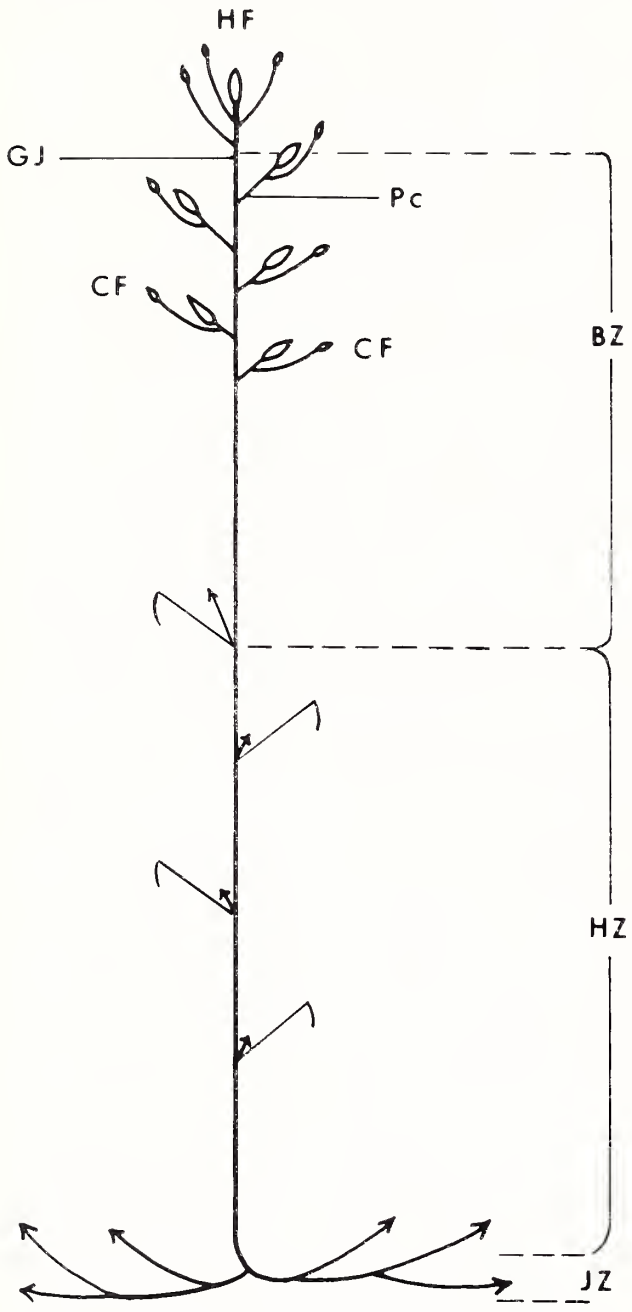

FIGURE 12.—Schematic of *Maclurolyra tecta.* [*BZ*=supplementing zone, *CF*=coflorescence; *GJ*=basal internode of the main florescence, *HF*=main florescence, *HZ*=inhibition zone, *JZ*=innovation zone, *Pc*=paracladium.]

We consider our analysis of the synflorescence of *Maclurolyra* as tentative only. Further studies, especially developmental, of the inflorescence of this genus and the other genera of the tribe, are needed before our conclusions here can be substantiated.

Floral Features

Lodicules

Taxonomic significance has been given to lodicules on the basis of several studies made from the point of view of morphology, anatomy, and ontogeny. Recently, some taxonomists have summarized the results of these investigations. Stebbins (1956) recognized four lodicule types: bambusoid, festucoid, panicoid, and chloridoid. Decker (1964) reported the previously unpublished conclusions of Reeder, who had also found four types: bambusoid (bamboos and a few related genera), festucoid, panicoid (Paniceae, chloridoid-eragrostoid, arundinoid-danthonioid, and the centothecoid groups of grasses), and a fourth type found in the Meliceae. Tateoka (1967) described the structure of lodicules of *Aristida, Stipa,* and the tribe Ehrharteae. Hsu (1965) pointed out several distinctive features in the lodicules of *Panicum.* Tateoka and Takagi (1967) described the anatomical features of the epidermis of lodicules, including those of several tribes of the Bambusoideae. Anatomical studies on bamboo lodicules were also reported by Takagi (1964, 1967, 1968) and Dobrotvorskaya (1962).

It should be noted that lodicules show a strong change in their thickness depending on whether observed in the fresh, fixed, or in the dried condi-

tion. In the case of dried specimens, lodicules were examined prior to treatment with a wetting agent (in this case Aerosol OT Solution). Although the lodicules became softer they did not regain their normal texture but rather appeared thin and membranous. Those of *Olyra latifolia* have been reported by Hsu (1965:94) as "papery," a description probably based on herbarium material. In all of the preserved material of *O. latifolia* that we examined the lodicules were fleshy.

Butzin (1965:35), in his anatomical description of the spikelet of *Olyra cordifolia,* pointed out that the posterior lodicule is fused at its base with the palea. In our studies of olyroid grasses (Calderón and Soderstrom, 1967) we found that in several species of *Olyra, Piresia,* and *Cryptochloa,* the back lodicule becomes detached at a higher level than the other two and shows a certain degree of fusion with the palea. A similar condition seems to prevail in the bamboos in which, according to McClure (1966:114), the posterior lodicule is addorsed to the palea.

The lodicules of *Maclurolyra* (Figure 7*j,k,r,s*) possess a number of features which are in agreement with the already-established "bambusoid" type. The number of three, the size, and the degree of vascularization are unquestionably bambusoid features. However, the lodicules of *Maclurolyra,* along with those of the Olyreae, diverge from those of the bamboos in their shape and anatomical features of the epidermis. Microhairs, stomata, and siliceous cells, which are found in the epidermis of bamboo lodicules, are lacking in *Maclurolyra* and the Olyreae (so far with the exception of *Olyra latifolia* whose lodicules sometimes possess microhairs along the upper margin).

The shape of the upper margin (more or less truncate), the vascularization, and the texture of the lodicules of *Maclurolyra* and the Olyreae resemble more those of the panicoid type. But, on the other hand, they differ from panicoid lodicules in that they are three in number, not plicate, and are usually larger in size.

The following combination of features allows us to establish the "olyroid" type of lodicule. We consider this to be a subtype of the bambusoid type of lodicule, and is characteristic of genera of the Olyreae, including *Maclurolyra*: lodicules three in number, more or less oblong with an irregularly truncate apex, not plicate, fleshy throughout with well-developed vascularization, epidermis lacking stomata, siliceous cells, and microhairs (except in rare instances where they occur along the upper margins).

Staminodes

In genera of the Bambusoideae, the occurrence of staminodes is rather frequent. It is interesting to find them reported for two herbaceous African genera with bisexual flowers, *Puelia* and *Atractocarpa* (Jacques-Félix, 1962:118–119; cf Clayton, 1966, 1967). Holttum (1958:22–23) recorded for the Asiatic bamboo, *Schizostachyum,* the occurrence of transitional forms between stamens and lodicules and drew attention to this phenomenon as evidence of the petaloid nature of lodicules.

Staminodes have also been observed by several investigators in the unisexual flowers of genera belonging to the Olyreae. Stapf (1906:204) described *Diandrolyra bicolor* as having female flowers with two staminodes only, the third aborted. Pilger (1915:167) mentioned the presence of three staminodes in female flowers of *Buergersiochloa.* Butzin (1965:35) found the same situation (three nerveless staminodes) in the female flower of *Olyra cordifolia.*

In our investigations we have found staminodes in several species of *Olyra, Cryptochloa, Bulbulus,* and others. In *Diandrolyra* we found the staminodes to be vascularized.

Pariana has been described by Doell (1883:331) as having five lodicules in both the female and the male flowers. Bentham (1881:24) gave a different interpretation to the five lodicules of the same genus; for him they were rudimentary staminodes. Butzin (1965:36) gave an account of the female flower of *Pharus glaber.* He found five rudimentary structures around the ovary, two of them considered as small lodicules and the remaining three as a verticil of stamens.

Staminodes are always present in the female flower of *Maclurolyra* (Figures 7*j,k,o,* 13*a,b,e,f*) and frequently also in the male. In the former case they appear as three scaly formations which are sometimes well developed, are arranged in a single verticil, alternate with the lodicules, and are situated at a higher level, just below the gynoecium. In this particular case the use of the word "staminode" seems most appropriate as these structures seem to represent a vestige of the staminal verticil which is

missing. In the male flower the designation of these structures is more difficult and depends on interpretation. On one hand they could represent an atrophied verticil of stamens, based on the hypothesis that the primitive grass flower has six stamens, alternating in two verticils. According to this hypothesis, a flower of three stamens is derived from one of six by loss of the internal verticil (Arber, 1934:120, 140). In *Maclurolyra* the reduction seems to have affected the external whorl, a situation which does not corroborate such an hypothesis. On the other hand, one could assume that these structures represent a rudimentary internal verticil of lodicules. Taking into consideration the typical floral diagram of the Monocotyledonae, Arber (1934:149) felt that the lodicules in the Gramineae represent the members of the interal verticil of a perianth of two verticils in which the external one has been lost. In the male flower of *Maclurolyra* these scaly formations are found *between* the lodicules and stamens. Arber (1927) described in detail the frequency of structures (appendages) intermediate between lodicules and stamens in hermaphrodite flowers of several Bambuseae, which she referred to as "stamen-lodicules." In order to facilitate the description of these structures in the present paper, the term "staminode" is used, but this is not meant to imply any morphological interpretation. We consider it premature to assign them definitely to one or the other structure at this time.

Gynoecium

Development.—During the course of its development the gynoecium undergoes progressive changes in size and shape. In its early stages, when it is about 5 mm long, it has the shape of a short bottle and the ovary is ovoid or nearly spherical with very thick walls (Figure 13*a,b*). The style is almost conical with two short, blunt, erect, closely appressed stigmatic branches. At this early stage there are no hairs on the style. In a later stage of development, the base of the style immediately above the apex of the ovary is covered by hairs on the front and back surfaces (Figure 7*p,q*), with the narrow sides glabrous. A rapid increase in length takes place in the style and later in the stigmatic branches, this occurring mainly at the base of the style and above the hairy zone. This elongation causes the hairy zone to be displaced upward (Figure 7*o*). In a well developed gynoecium—even prior to fecundation—the style is composed of a proximal glabrous zone of about 1.3–1.6 mm long, a median one about 1.8–2.4 mm long with hairs, and a distal one which is slender and glabrous (Figure 7*o*). The stigmatic branches also enlarge rapidly and increase in length. At maturity the gynoecium has elongated considerably and has a style 8–12 mm long.

Hairs of the Style.—When the gynoecium has reached maturity, the hairs of the style are also completely developed. This area is densely covered for the most part by long macrohairs (Figure 15*b,h*) with thick walls. The hairy zone in the upper part of this zone terminates in a small extension covered by short marcrohairs or hooks (Figures 14*a*, 15*a,g*.).

Microhairs and long multicellular (4–celled) hairs (Figure 15*c*) are also present on the style, as observed under high magnification. They are found mostly at the base of the hairy zone and between the macrohairs. Most of them are tricellular (Figures 14*b*; 15*e*) and a few bicellular (Figure 15*d,f*). The former are 80–109 microns long, more or less uniform in diameter, with the distal cell a little shorter than the basal ones and with a rounded or slightly tapered tip. The two basal cells have much thicker walls than the apical one. The bicellular microhairs are about 112 microns long, are also more or less uniform in diameter, but the distal cell is longer than the basal one, and is rounded at the tip. It is thin-walled as opposed to the basal cell which is thick-walled.

Intermixed with the macrohairs and microhairs are long 4-celled hairs (Figure 15*c*) which occur mainly in the lower half of the hairy zone. These measure about 333 microns long, the constituent cells are of about equal size, have very thin walls, and are pointed at the tip. By customary interpretation of these terms, such hairs cannot be regarded as either macrohairs or microhairs. The distinction between both kinds of hairs is based on their size,

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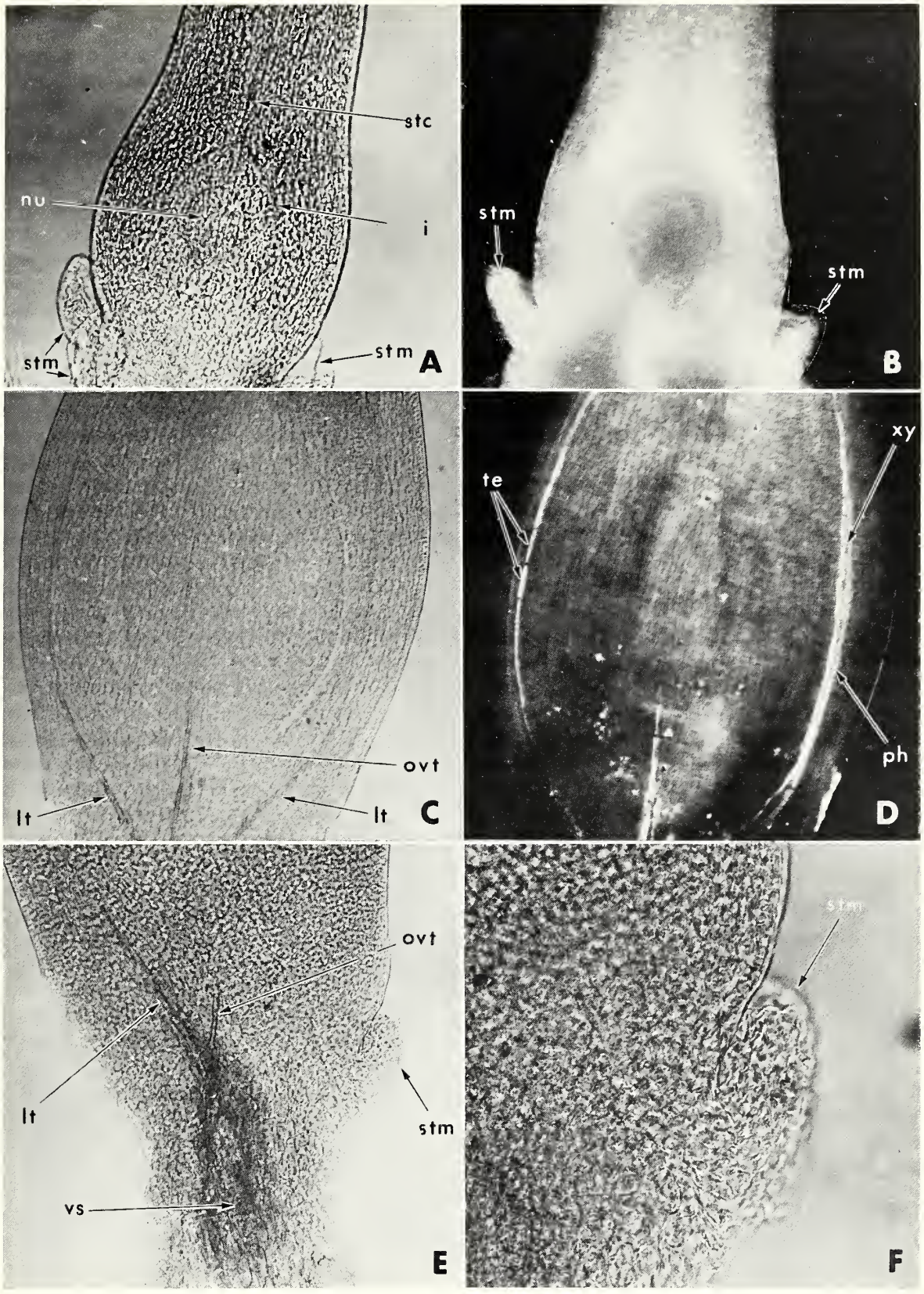
Figure 13.—Photomicrographs of the gynoecium of *Maclurolyra tecta*. [*i*=integuments, *lt*=lateral trace, *nu*=nucellus, *ovt*=ovule trace, *ph*=phloem, *stc*=stylar core, *stm*=staminodes, *te*=tracheary elements, *vs*=vascular supply of the gynoecium, *xy*=xylem.] Photomicrographs A, E, and F were taken with phase contrast illumination, B with dark field, C with bright field, and D with polarized light. Magnifications: A and B, ×125; C-E, ×312; F, ×500.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number of cells, and shape of the tip of the single or distal cell. Microhairs are very small, 2–several-celled, and the basal cell or cells are thicker walled than the distal cell which is thin-walled. Macrohairs, on the other hand, are much larger, single-celled, and have a uniformly thick wall. Tateoka and Takagi (1967), in their discussion of lodicule hairs, consider the shape of the hair apex as a distinguishing character. The distal cell in microhairs is rounded or blunt at the tip while the apex of macrohairs is pointed.

Multicellular microhairs have been observed in the epidermis of lodicules of several species of bamboo (*Pseudosasa, Chimonobambusa, Sasa, Bambusa, Arundinaria, Pleioblastus*) by Tateoka and Takagi (1967). Takagi (1967, 1968) reported mircohairs made up of 4–6 cells in some species of *Sasa* and *Sinobambusa*. These multicellular hairs are regarded as microhairs and most of the illustrations show that they are similar to bicellular microhairs in that they are small, the basal cell is thick-walled, and the two or three apical cells are thin-walled and rounded at the tips.

Microhairs made up of three, four, or several cells also occur in the leaf epidermis of some bamboos, but such hairs seem to be most common in the epidermis of the lodicules. We have not yet found multicellular microhairs of this type in any species of the Olyreae.

The 4-celled hairs found on the style of *Maclurolyra* are unlike multicellular microhairs in that the walls of all cells are thin and the hairs are much longer and pointed at the tip. In length they approach that of some macrohairs, but differ from macrohairs in that they have more than one cell and are not thick-walled. Since these 4-celled hairs do not correspond to either microhairs or macrohairs, we refer to them as "isoleptoid" hairs in allusion to the equal size of all cells in the hair and the fact that each is thin-walled. The name is derived from the Greek words *isos,* meaning "equal," and *leptos,* meaning "thin." We have not encountered isoleptoid hairs or multicellular microhairs in any other genus of the Olyreae. Takenouchi (1931a) figures multicellular hairs for the epidermis of prophylla of many species of Japanese bamboos. These cells are pointed at the tip but the measurements he gives show them to be much shorter than the isoleptoid hairs of *Maclurolyra*. Since he does not give any details concerning these hairs we cannot assign them to any particular type.

Vascularization.—The vascular system of the bamboo gynoecium is usually composed of four bundles, one posterior or placental strand, two lateral-posterior bundles, and a median-anterior one. Five or six traces are also very frequent in the bamboos. Arber (1926, 1927) reported ovaries with six traces in species of *Bambusa, Gigantochloa,* and *Cephalostachyum.*

In *Maclurolyra,* the number of vascular traces in the gynoecium is three (Figure 13*c,d*), these arising from the single main trace (Figure 13*e*) which enters the ovary at its base. Of the three traces one is a posterior placental strand which supplies the ovule (Figure 13*c-e*). It is represented by an arc of vascular elements which terminates shortly after entering the ovule. The remaining two small lateral bundles run up through the ovary walls, enter the style, and pass into the stigmas. Both xylem and phloem are present in these bundles (Figure 13*d*).

A gynoecium with three vascular traces seems to be the general rule for the Olyreae, as we have found this condition in several species of *Bulbulus, Cryptochloa, Olyra, Piresia,* and *Reitzia.*

Ovule Morphology.—The ovule is semianatropous or anacampylotropous (Bocquet, 1959), bitegmic, and the micropyle is formed by the inner integument. This integument is composed of two layers of cells in most of its extension, becoming thicker (Figure 16*b,c*) to form the micropyle which covers the nucellus completely. Figure 16*b,c,* shows a partially dissected ovule in which the micropyle is seen facing downward. In an early stage of the ovule development (Figure 13*a,b*) the two integuments cover the nucellus. A later stage of development is shown in Figures 13*c* and 16*a-c,* where the outer integument can no longer be distinguished clearly.

The top of the ovule has a cap-shaped formation ("apical formation") which probably represents the outer integument reduced (Figure 16*a-d*). A short strand of tissue ("connecting strand," Figure 16 *b-d*) connects this upper part of the ovule with

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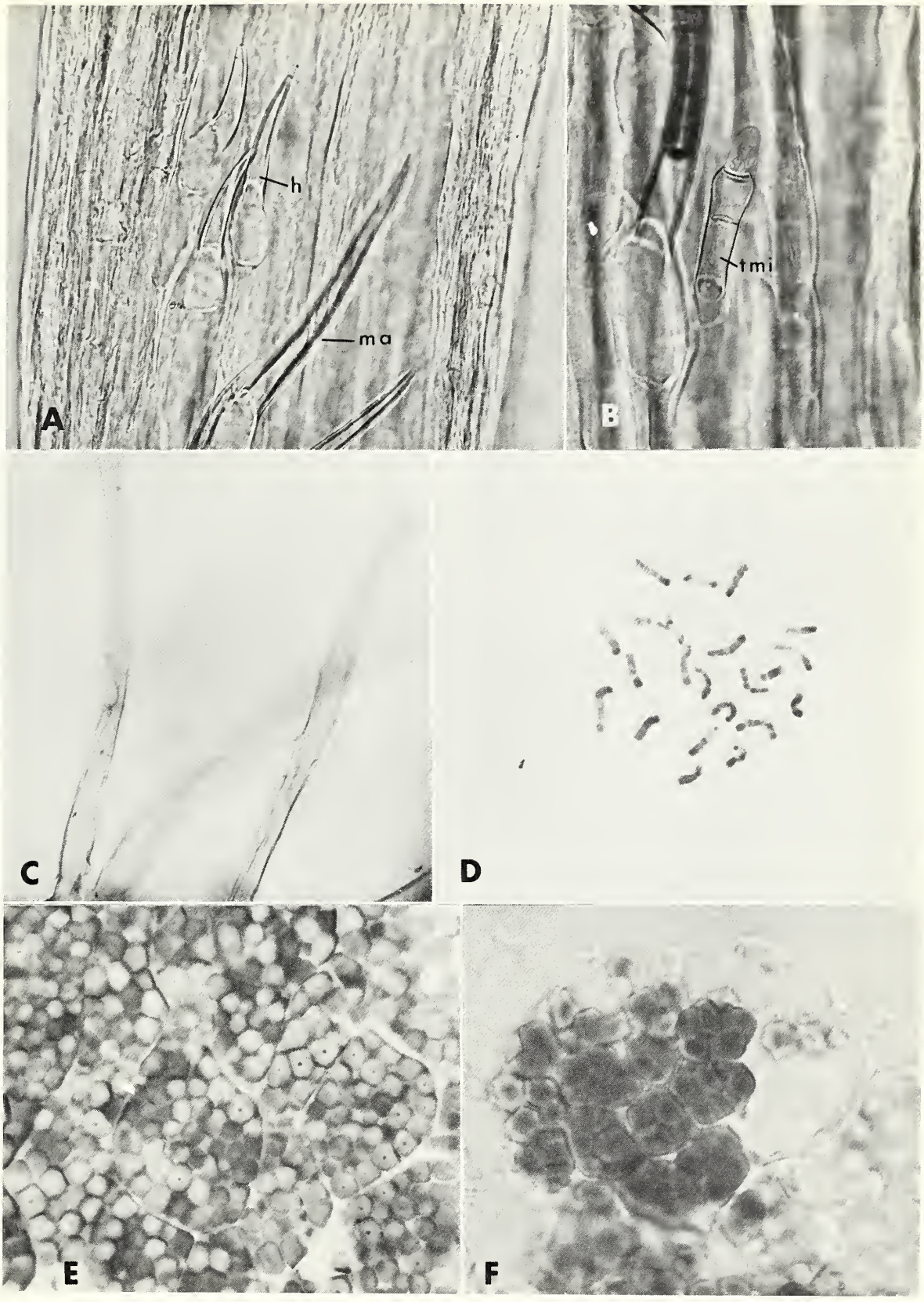
Figure 14.—Photomicrographs of *Maclurolyra tecta*: A, B, style; C, fusoid cells from preparation of dissociated tissue; D, chromosomes in somatic metaphase in young anther, 2n =22; F, simple starch grains of *Cephalostachyum burmanicum*; F, compound starch grains of *Maclurolyra tecta*. [*h*=hook, *ma*=small macrohair, *tmi*=tricellular microhair.] Magnifications: A-C, ×600; D, ×1500; E and F, ×450.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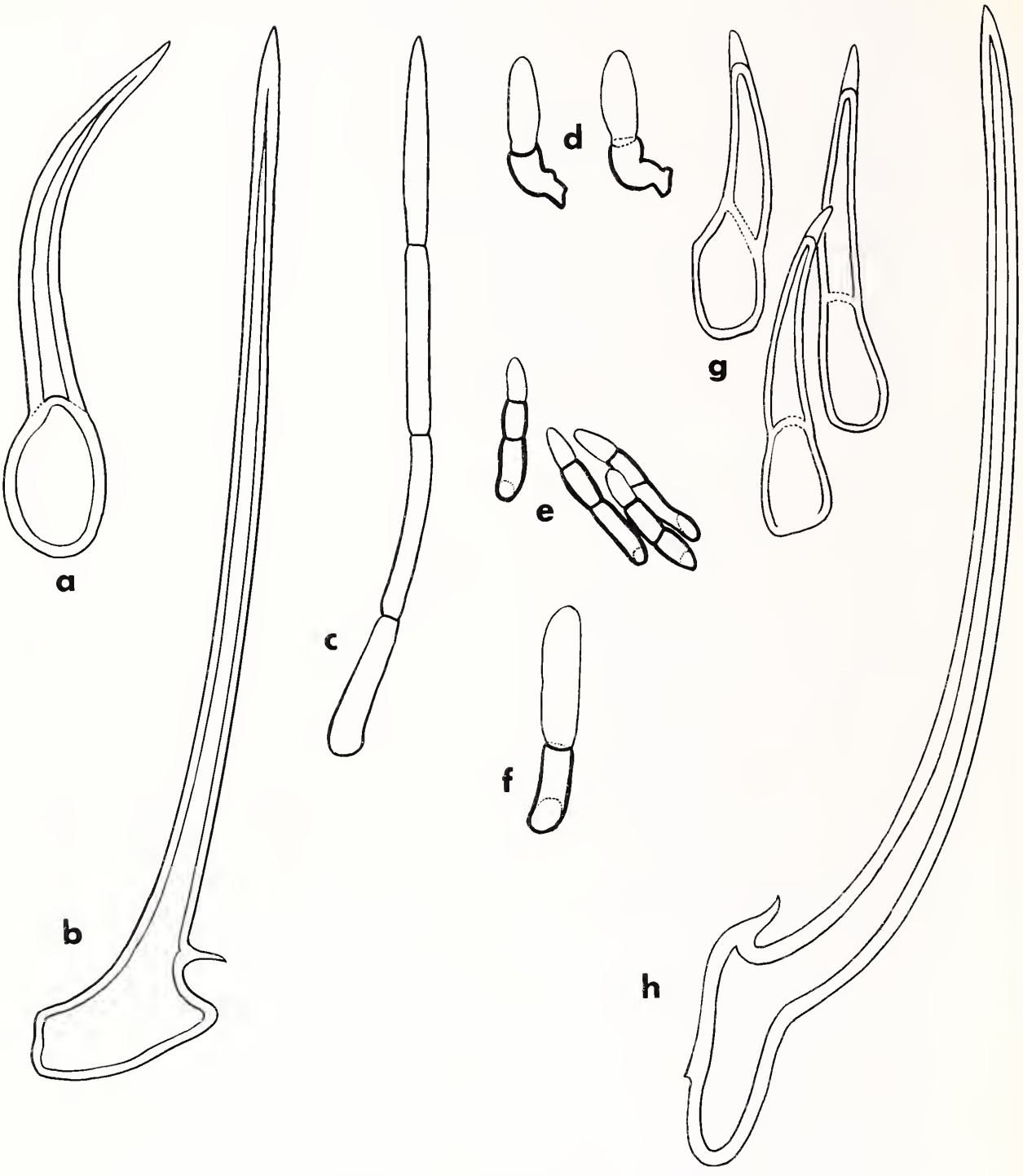

FIGURE 15.—Stylar hairs of *Maclurolyra tecta*: *a*, Small macrohair; *b*, large macrohair; *c*, isoleptoid hair; *d*, bicellular microhairs; *e*, tricellular microhairs; *f*, bicellular microhair; *g*, hooks; *h*, large macrohair. All drawings ×560.

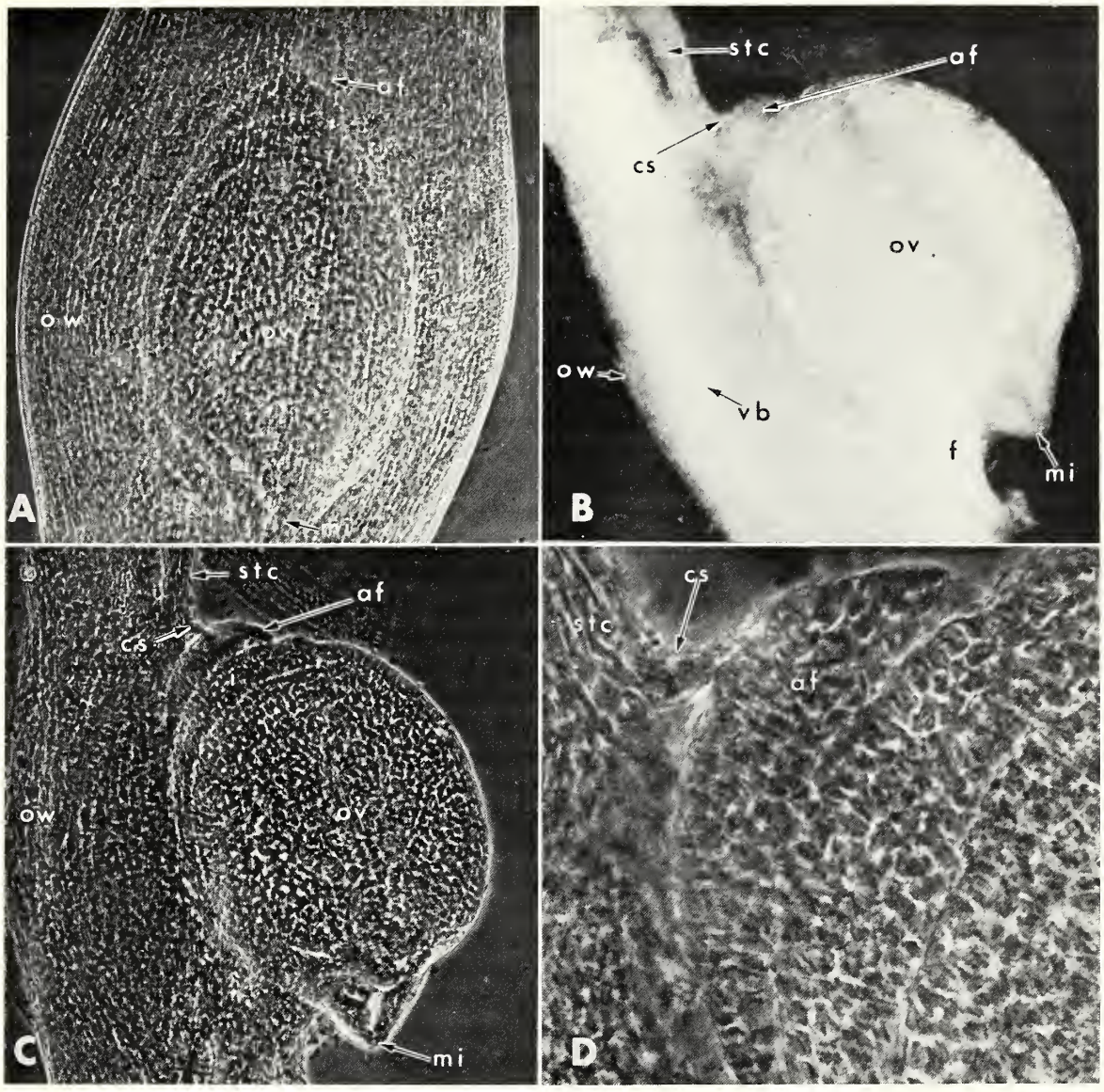

FIGURE 16.—Photomicrographs of the ovule of *Maclurolyra tecta*. [*af*=apical formation, *cs*=connecting strand, *f*=funiculus, *i*=integument, *mi*=micropyle, *ov*=ovule, *ow*=ovary wall, *stc*=stylar core, *vb*=vascular bundle.] Photomicrographs A, C, and D were taken with phase contrast illumination, and B with dark field. Magnifications: A-C, ×312; D, ×500.

a central strand of tissue of the style (Figure 16*b-d*). This central portion of the style is referred to by Arber (1934) as a stylar core (Figure 16*b-d*). However, the nature and interpretation of these structures still remain to be investigated.

Cytology

Chromosome counts of bambusoid grasses are not so numerous as they are for other grasses. Those which have been reported for bamboos indicate that most species are tetraploids, based on x = 12. Chromosome counts for bamboos appear in widely scattered publications, but a couple of references which deal solely with bamboos are Janaki Ammal (1959) and Uchikawa (1933, 1935).

A basic number of x = 12 has also been reported for the herbaceous bambusoid grasses *Neurolepis* (Gould and Soderstrom, 1970), *Pariana* (Reeder,

Soderstrom, and Calderón, 1969), and *Streptogyna* (Tateoka, 1958*b*; Veyret, 1958). This same basic number has also been reported for *Pharus* (Reeder, Soderstrom, and Calderón, 1969) and *Leptaspis* (Tateoka, 1958*b*), genera allied to the Bambusoideae but which we do not include within the subfamily.

A basic number of x = 11 has been reported for *Streptochaeta* (Valencia, 1962; Pohl and Davidse, 1971), a herbaceous bambusoid grass, and the tribe Olyreae, so far reported for the following members: *Lithachne pauciflora* (Pohl and Davidse, 1971), *Olyra latifolia* (Reeder, Soderstrom, and Calderón, 1969; Tateoka, 1962a [as *O. yucatana*]; Pohl and Davidse, 1971), *O. loretensis* (Gould and Soderstrom, 1970), *O. obliquifolia* (Gould and Soderstrom, 1970) *Piresia goeldii* (Gould and Soderstrom, 1967), and *Raddia costaricensis* (Pohl and Davidse, 1971, although Reeder, Soderstrom, and Calderón [1969] gave 2n = 24 for the same species).

Basic numbers lower than x = 11 have also been found in the Olyreae, e.g. x = 10 in *Bulbulus nervatus* (Gould and Soderstrom, 1967), *Olyra micrantha* (Gould and Soderstrom, 1967), and x = 9 in *Diandrolyra bicolor* (Daker, 1968, in which a karyological analysis is also given). Dr. Pierre Morisset (personal communication) relates that x = 7 (2n = 14) in *Olyra fasciculata* (based on *Calderón* 2024, previously unpublished).

A chromosome count of 2n = 22 (Figure 14*d*) was obtained from pollen mother cells of the type-collection of *Maclurolyra tecta*. We consider it to be a diploid based on x = 11 which basic number, in the Bambusoideae, conforms to that of many members of the tribe Olyreae.

Starch Grains

The taxonomic significance of differences in the morphology of starch grains in plants was early recognized by Fritzsche (1834). His work was followed by that of others such as Nägeli (1858), Harz (1880), and Reichert (1913). More recently Wagnon (1952) made use of starch grain differences in separating the grass genera *Bromus* and *Festuca*. An extensive study of starch grains, found in the endosperm of grasses belonging to 244 genera (comprising 766 species), was made by Tateoka (1962b). He recognized four types of starch grains but felt that their use was generally of minor significance in the taxonomy of the family.

Our own preliminary studies of starch grains in genera of the Bambusoideae, and especially the tribe Olyreae, indicate that they may be of different types between genera or between species within a genus. We believe that characters of the starch grains, used in conjunction with other characters, should prove to be of systematic value.

The starch grains of *Maclurolyra* (Figure 14*f*) are compound and correspond to Type IV of Tateoka, the type which he reported for the bamboos under his study. We have found compound grains in some genera of the Olyreae (*Bulbulus, Olyra, Piresia, Raddia, Reitzia*) and in some bamboos (*Oxytenanthera, Phyllostachys, Sinarundinaria, Thyrsostachys*). Yakovlev (1950:154) illustrated compound grains for *Olyra latifolia*. We have found simple starch grains (Type II of Tateoka) to occur as well in the Bambusoideae as, for example, in the Asiatic bamboo, *Cephalostachyum burmanicum*, shown here for comparison (Figure 14*e*).

Leaf Anatomy

In the anatomical and histological descriptions of the leaf blade we are following the order used by Metcalfe (1960), with minor modifications. These include the addition of the description of the adaxial epidermis and, in the transverse section, the description of the bundle sheath follows that of the vascular bundle.

The Epidermises

Abaxial Epidermis (Figure 17): Thick cutinized, with well differentiated costal zones above the veins and intercostal zones between them. Intercostal zones formed by three wide bands, two of stomata along the sides of the veins and one of long and short elements alternating with the stomatal bands.

Short Cells: Abundant all over; in the intercostal zone in pairs, over the veins mostly in long rows, some in short rows of five or six cells, sometimes in pairs.

Siliceous Cells: Between the veins transversally elongated, narrow and crenate, of the "olyroid" type (p. 36) with silica bodies smaller than the cells and of approximately the same shape, sometimes

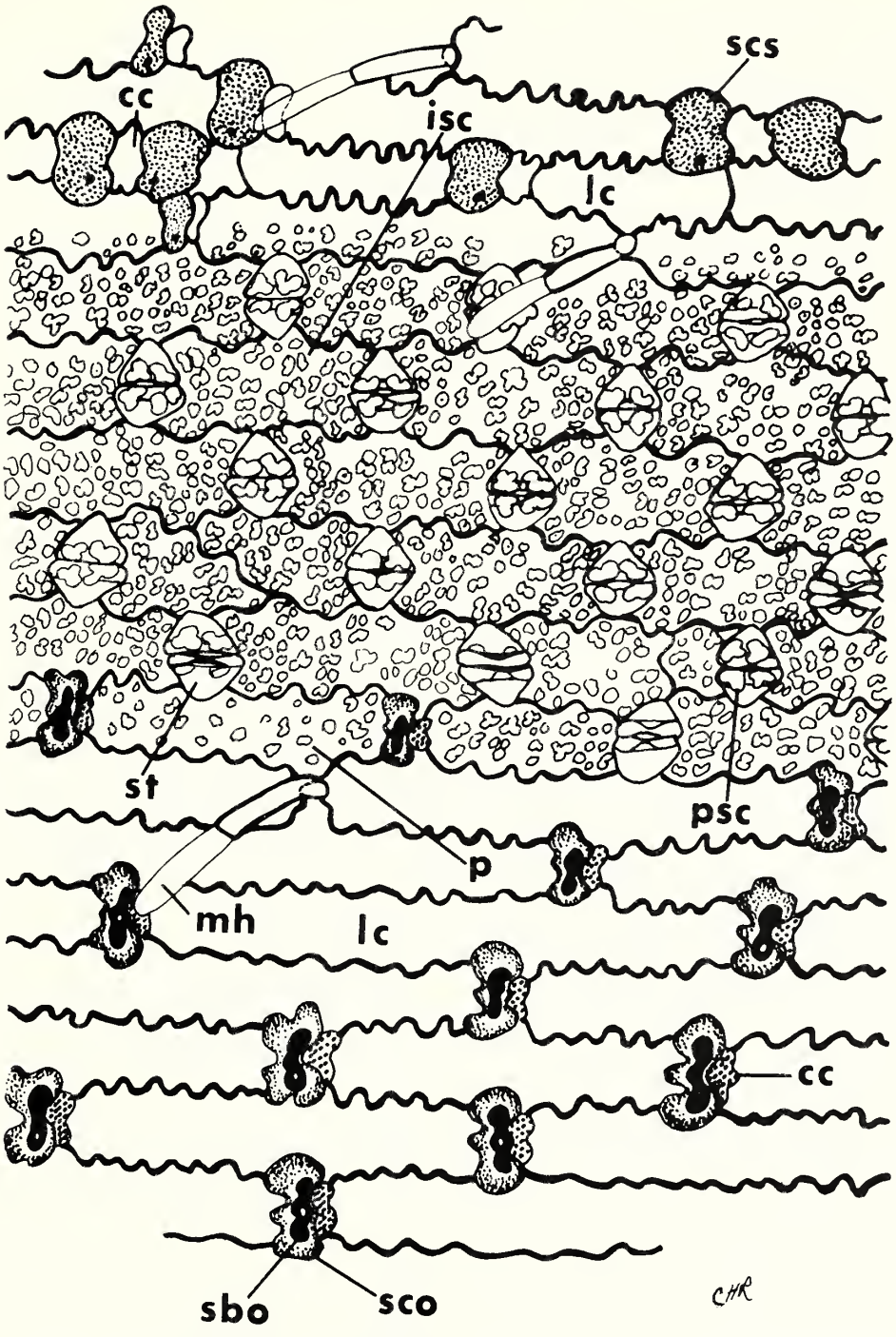

FIGURE 17.—Abaxial epidermis of the leaf blade of *Maclurolyra tecta*, ×600. [*cc*=suberin (cork) cell, *isc*=interstomatal cell, *lc*=long cell, *mh*=bicellular microhair, *p*=papilla, *psc*=papilla of subsidiary cell, *sbo*=silica body (olyroid type), *sco*=siliceous cell (olyroid type), *scs*=siliceous cell (saddle-shaped), *st*=stoma.]

slightly crenate or narrow in the middle, like a narrow oryzoid type of silica body. Siliceous cells over the veins large, with silica bodies that fill the cells completely, mostly in modified cross-shaped or intermediate between saddle-shaped and oryzoid type.

Suberin (Cork) Cells: Between the veins associated with a siliceous cell; very small, lobulate or crenate, about the same shape as the siliceous cell, sometimes outline obscure; those over the veins larger.

Macrohairs: None seen.

Prickle Hairs and Hooks: Along the edges on the upper half of the blade.

Microhairs: Bicellular, of the linear type, common in, or mainly flanking, the stomatal bands and on either side of the veins, but some in the interstomatal zone as well; frequently bent near their bases; distal cell thin-walled; usually uniform in diameter throughout their length, and with rounded apices or sometimes only slightly tapering towards a rounded point, with both cells of about equal length, but mostly with the distal cell slightly longer than the basal cell; hairs 48–66 (mostly 54–60) microns long; basal cells 20–32 (mostly 22–28) microns long; distal cells 26–34 (mostly 28–32) microns long.

Papillae: Abundant, present both in the stomatal bands and over the veins; rather small, variously shaped, irregularly rounded to triangular, with crenate outlines; very thick-walled and cuticularized or silicified; more than one row per cell; papillae abundant around the stomata, a variable number of them projecting above and overarching the individual stomata, thus obscuring the outlines of the subsidiary cells and the interstomatal cells as well.

Stomata: Numerous, occurring in bands of 4–6 rows of stomata that alternate with each other and restricted to the sides of the veins; usually only one interstomatal cell separating two stomata; stomata with triangular subsidiary cells, each one with two rounded-crenate, thick cuticular papillae, the stomatal opening being completely obscured by the 4 overarching papillae.

Long Cells: In the interstomatal bands with thick sinuous walls and devoid of papillae; each of the long cells in a single row separated by a pair of short cells or sometimes by a microhair; those over the veins slightly narrower.

Interstomatal Cells: With concave ends and markedly sinuous in outline, the cells rather shorter, some of them almost cubical; papillae very abundant.

Transverse Veinlets: Abundant, very conspicuous, connecting vascular bundles of all types and with a parenchymatic sheath.

Adaxial Epidermis (Figure 18): Very cutinized with bands of bulliform cells in the interstomatal zone and bands of long cells on both sides of the veins.

Short Cells: Abundant, over and between the veins, mostly in pairs; a few in rows of 3–5 or occasionally more cells, over the large veins.

Siliceous Cells: Between the veins only of the olyroid type, similar to those of the abaxial epidermis; silica bodies smaller than the cells, narrow and crenate. Siliceous cells over the veins with silica bodies mostly of the oryzoid type and saddle-shaped, some of the olyroid type or tending to be slightly cross-shaped.

Macrohairs: None seen.

Prickle Hairs and Hooks: See Abaxial Epidermis.

Microhairs: Abundant in the intercostal zone adjacent to the veins; of the same type as those on the abaxial epidermis; microhairs more numerous in this epidermis than in the abaxial one.

Papillae: Absent on both long cells and bulliform cells.

Stomata: Absent or very occasionally some present in the bands of long cells.

Bulliform Cells: In bands of 3–5 rows of cells wide in the middle of the intercostal zones; inflated cells, varying in appearance with the focus, short and broad to somewhat circular in outline; with very thick and strongly undulating walls.

Long Cells: In bands, on either side of the veins, formed by 7–9 rows of cells, each cell alternating with a pair of short elements or a microhair; with very thick and sinuous walls, sinuations strongly marked, more so than in the corresponding cells of the abaxial epidermis; long cells over the veins narrower.

The Transverse Section of the Lamina

Figures 19, 20, 21*a*, *b*, *d*

Leaf blade expanded in transverse section, both epidermal surfaces slightly undulated. Adaxial

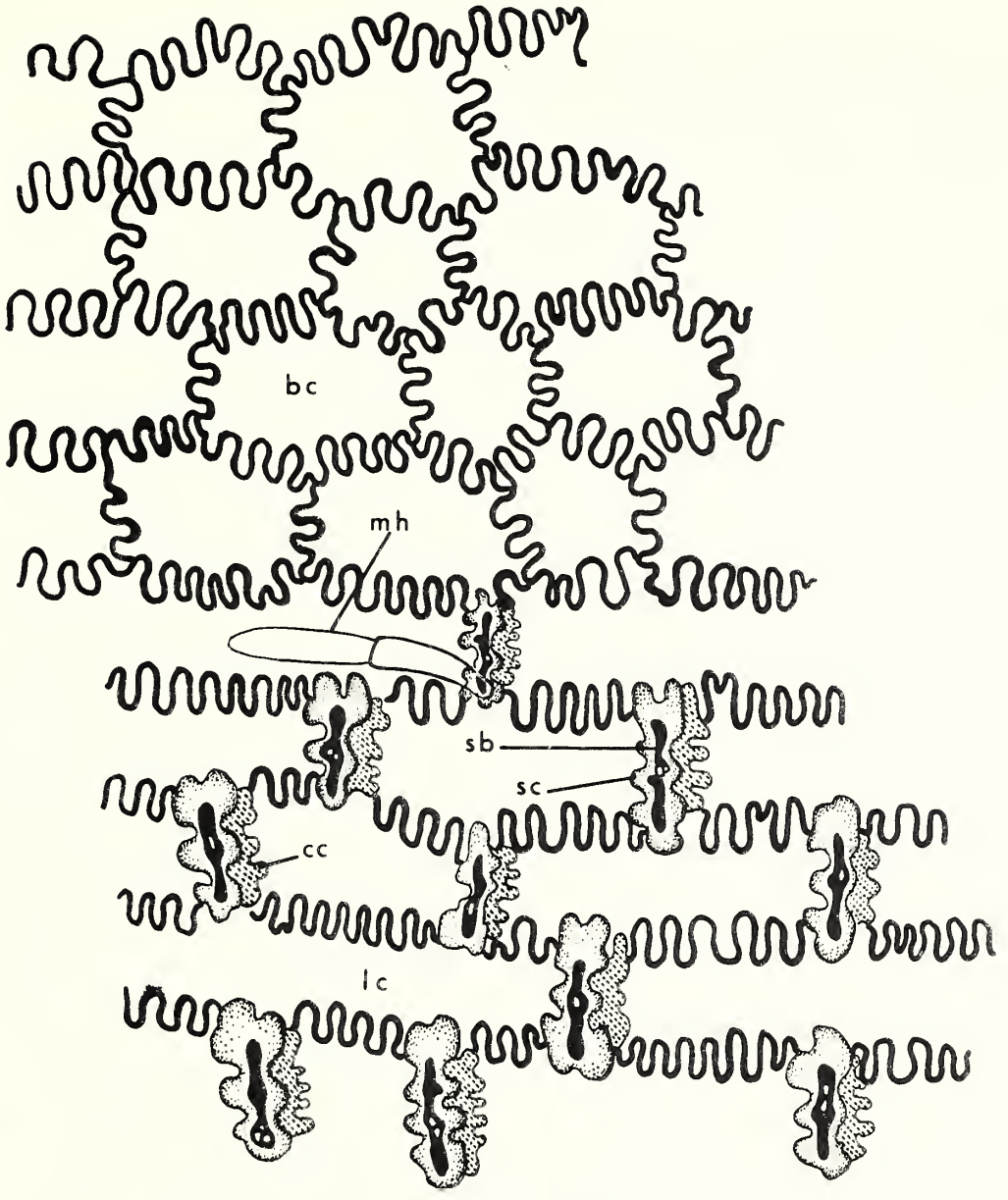

FIGURE 18.—Adaxial epidermis of the leaf blade of *Maclurolyra tecta*, ×600. [*bc*=bulliform cell, *cc*=suberin (cork) cell, *lc*=long cell, *mh*=bicellular microhair; *sb*=silica body (olyroid type), *sc*=siliceous cell (olyroid type).]

SURFACE with fairly wide ribs with rounded apices separated from one another by wide, very shallow furrows; the ribs over the large vascular bundles slightly more protruding; furrows on each side of the midrib most marked. ABAXIAL SURFACE less undulating than the adaxial one; ribs of the abaxial surface corresponding to the furrows of the adaxial surface; the slightly rounded ribs corresponding to the bulliform cells and the very shallow furrows corresponding to the vascular bundle units.

VASCULAR BUNDLE UNITS: Fairly widely spaced and not conspicuously angular in outline; about 7–9 first order vascular bundles present on either side of the midrib; small vascular bundles in groups of usually 5–7 alternating with the first order vascular bundles. FIRST ORDER VASCULAR BUNDLES

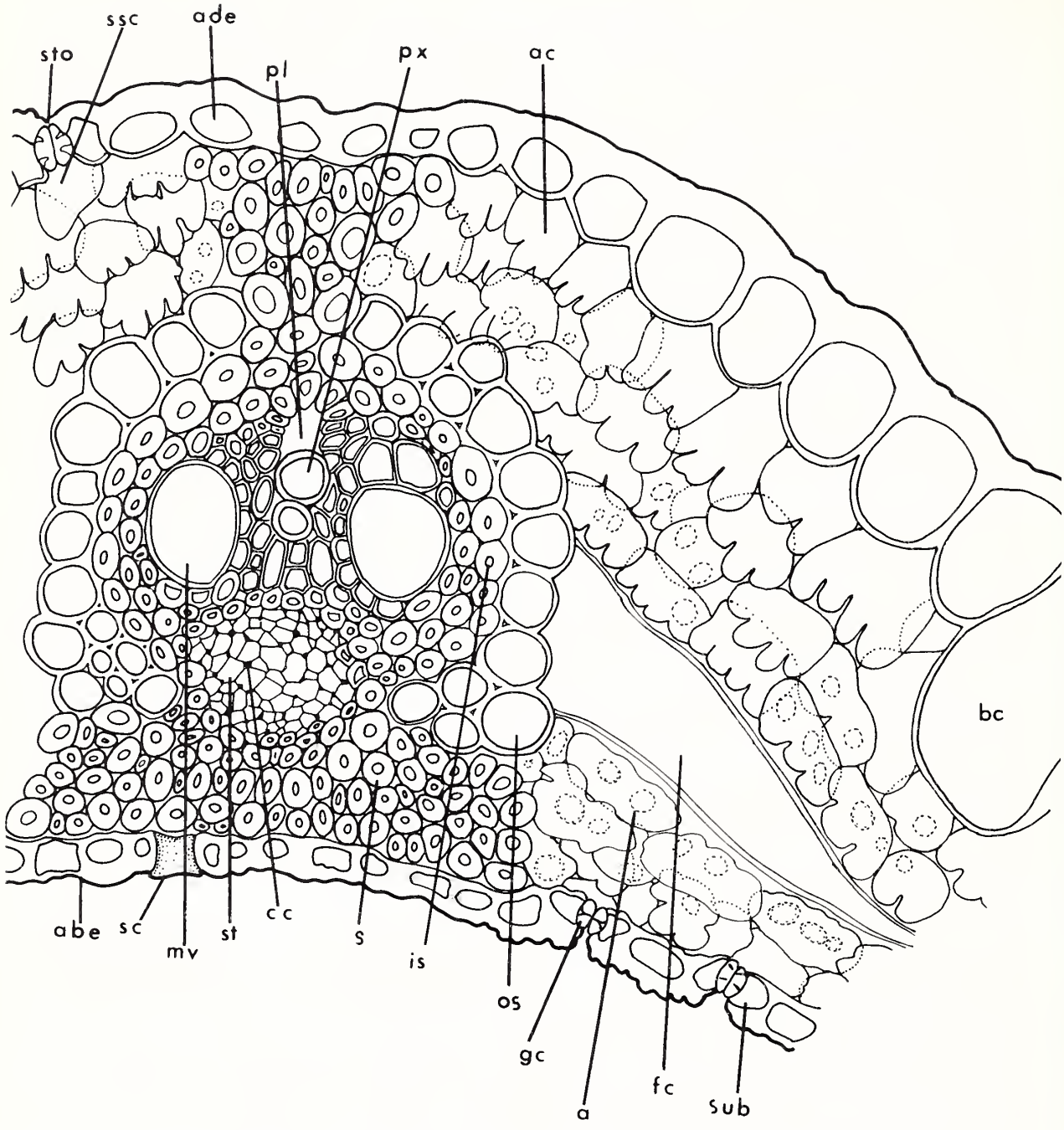

FIGURE 19.—Transverse section of a blade of *Maclurolyra tecta* through the region of a first-order bundle, ×600. [*a*=arm of arm cell, *abe*=abaxial epidermis, *ac*=arm cell, *ade*=adaxial epidermis, *bc*=bulliform cell, *cc*=companion cell, *fc*=fusoid cell, *gc*=guard cell, *is*=inner bundle sheath, *mv*=large metaxylem vessel, *os*=outer bundle sheath, *pl*=protoxylem lacuna, *px*=protoxylem vessel, *s*=sclerenchyma, *sc*=siliceous cell, *ssc*=substomatal chamber, *st*=sieve tube, *sto*=stoma, *sub*=subsidiary cell.]

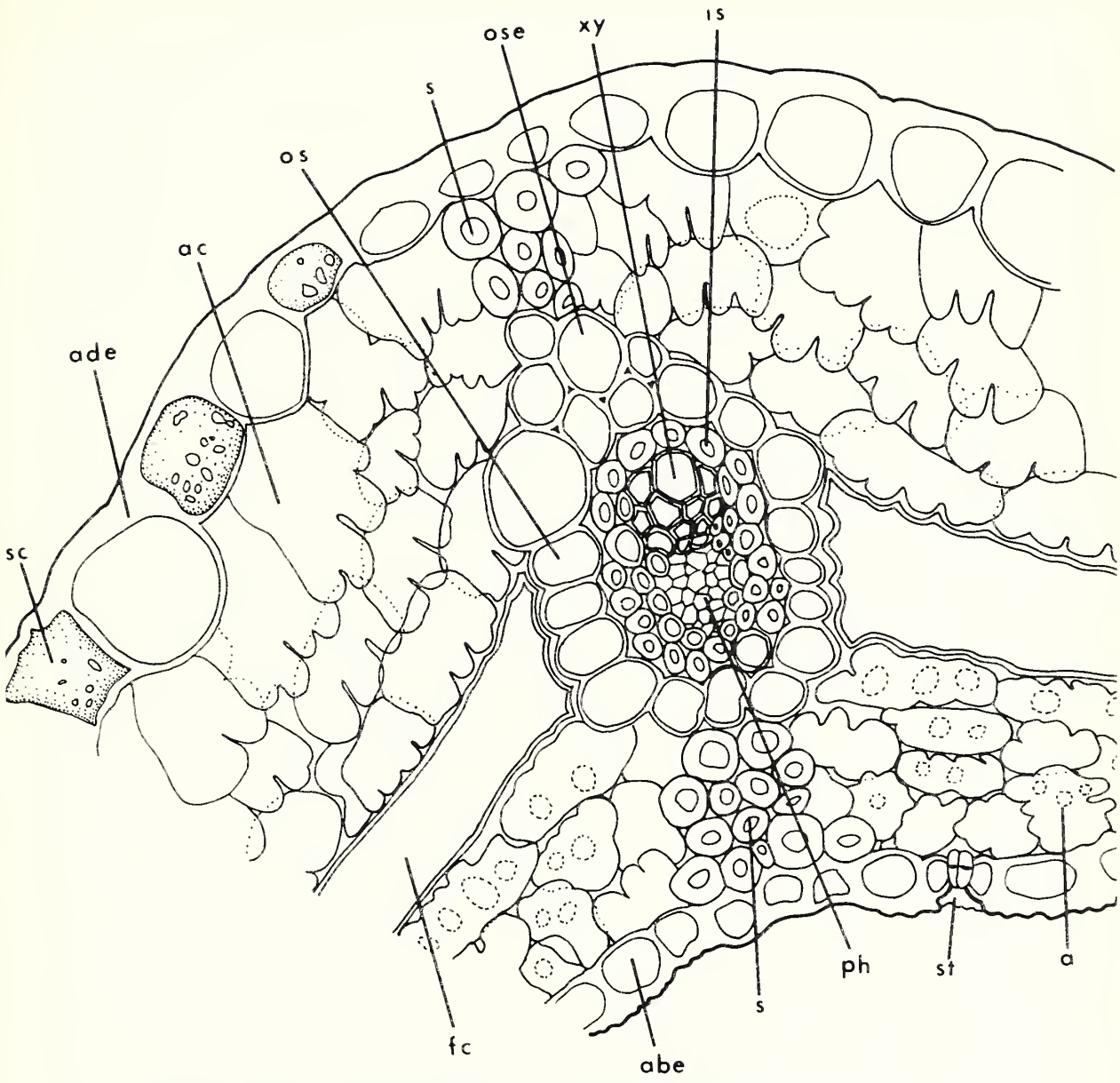

FIGURE 20.—Transverse section of a blade of *Maclurolyra tecta* through the region of a small bundle, ×600. [*a*=arm of arm cell, as seen from above, *abe*=abaxial epidermis, *ac*=arm cell, *ade*=adaxial epidermis, *fc*=fusoid cell, *is*=inner bundle sheath, *os*=outer bundle sheath, *ose*=outer bundle sheath extension, *ph*=phloem, *s*=sclerenchyma, *sc*=siliceous cell, *st*=stoma, *xy*=xylem.]

somewhat hexagonal in outline (the "basic type" of Metcalfe, 1960); large metaxylem vessels present; a ring of fibers encircling the phloem, separating it from the xylem, and continuing, without transition, to the inner sheath and the abaxial sclerenchyma girder. SMALL VASCULAR BUNDLES somewhat oval or oblong in outline, xylem and phloem well differentiated; xylem elements fairly wide in diameter, but no large metaxylem vessels present.

BUNDLE SHEATH: Double; small vascular bundles with two complete sheaths, the outer sheath often having a slight extension of parenchymatic cells, sometimes 1 to 3 cells, connecting with the adaxial sclerenchyma; first order vascular bundles with the

outer sheath interrupted abaxially, some first order bundles also with a small, 1 or 2 cells wide, adaxial interruption; abaxial interruption rather wide. The outer sheath in all bundles conscipuous and consisting of parenchymatous cells with slightly thickened walls, rather wide in diameter and containing few small chloroplasts. The inner sheath very conspicuous and complete in all bundles although in the first order bundles somewhat obscure on the abaxial side and merging into the adjacent sclerenchyma. In transverse section cells of the inner sheath roundish, much smaller in diameter than those of the outer sheath, conspicuously pitted, with strongly and uniformly thickened walls. In all vascular bundles, but mainly in the first order bundles, the inner sheath almost double, having the appearance of a thick ring encircling the conductive elements. Vascular bundles of the midrib completely enveloped by a sheath of highly lignified fibers; sheaths about 2 or 3 cells wide in the lateral bundles and about 3 or 4 cells wide in the median bundle. Small lateral bundles of the midrib region with a complete outer sheath; median bundle with outer sheath not clearly differentiated from the surrounding ground tissue.

Midrib: Very conspicuous owing to a large, rounded and flat-topped adaxial, and a rounded and a much smaller abaxial, projection; containing near the abaxial side one large median vascular bundle and 2 smaller laterals, present on either side, sometimes 2 on one side and 1 on the other side. The median bundle and one lateral bundle connected by girders to the abaxial plate of sclerenchyma, sometimes the three vascular bundles of the keel with abaxial girders. The whole group of vascular bundles embedded in the mass of large-celled ground tissue of the midrib. A zone, several layers thick, of chlorenchyma (arm cells) present on either side of the adaxial projection, between the ground tissue and the epidermis.

Sclerenchyma: All vascular bundles with small adaxial and abaxial girders; those of the small bundles being somewhat triangular in shape, the abaxial girders slightly larger, about 5 or 6 cells wide and 3 or 4 cells high; adaxial girders smaller, about 2–5 cells wide and 3 cells high, girders of the first order vascular bundles more robust, about 14–18 cells wide by 2–4 cells high in the abaxial side; adaxial girders much smaller, about 6–10 cells wide by 3 or 4 cells high, combined girders somewhat anchor-shaped. Midrib supported by a thick and wide plate of sclerenchyma in the adaxial projection and a narrower mass of sclerenchyma in the abaxial rib; tall and rather narrow girders connecting this abaxial plate to the median bundle and one lateral bundle.

Mesophyll: Chlorenchyma not radiate, consisting of arm cells and fusoid cells occupying the center of the lamina in the intercostal zones.

Arm cells (Figures 21*b*, 22 *c,d*): Arranged in 3 or 4 horizontal layers below the adaxial epidermis and 2 or 3 layers above the abaxial epidermis. Cells flat, irregularly oblong or rectangular in outline, with rounded edges and typical invaginations of the cell walls extending to less than half the depth of the lumina of the cell; 3–5 projecting, rounded folds in each cell. In transverse section of the blade the orientation of the arm cells differing in both the adaxial and abaxial zones. In the adaxial layers most of the cells arranged with the folds or "arms" perpendicular to the epidermis, thus, in the sections the broad face of the cells showing and the "arms" proceeding from the lower edge. In the abaxial layers the "arms" parallel to the epidermis and only the unfolded, back edge of the cell seen, the outline of the folds appearing by transparence as bright circles or rings (Figures 19, 20). The arrangement of the chlorenchyma cells tending to be slightly irregular in the areas surrounding the vascular bundles. Arm cells between two fusoid cells rather smaller and with arms irregularly oriented. Chlorenchyma cells of the midrib small, and with arms apparently proceeding from all four edges.

Fusoid Cells (Figures 14*c*, 21*b,c*): Translucent, large and conspicuous; a single cell present on either side of each of the vascular bundles, the tall

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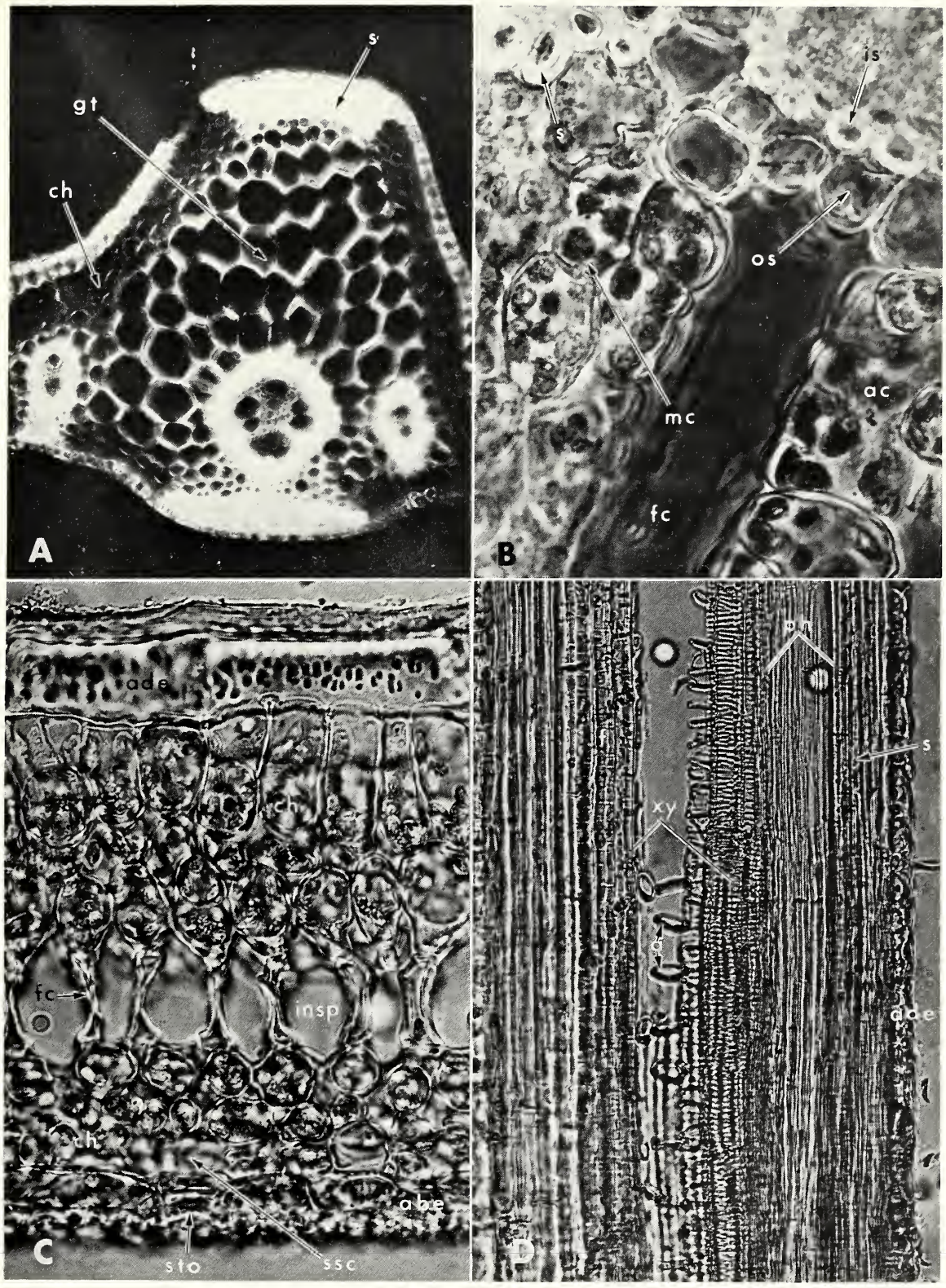
Figure 21.—Photomicrographs of leaf sections of *Maclurolyra tecta*: A, Midrib of blade; B, transverse section of blade oriented almost vertically (the adaxial side toward the right); C, longitudinal section through the mesophyll with the fusoid cells appearing in cross-section; D, longitudinal section through a vascular bundle. [*a*=annular thickenings of tracheary element; *abe*=abaxial epidermis; *ac*=arm cell; *ade*=adaxial epidermis; *ch*=chlorenchyma; f=fibers; fc=fusoid cell; *gt*=ground tissue; *insp*=intercellular space; *is*=inner bundle sheath; *mc*=mesophyll chloroplast; *os*=outer bundle sheath; *ph*=phloem; *s*=sclerenchyma; *ssc*=substomatal chamber; *sto*=stoma; *xy*=xylem.] Photomicrograph A was taken with polarized light; B with phase contrast illumination, and C and D with bright field. Magnifications: A, ×125; B-D, ×600.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edge of the cell in contact with the outer bundle sheath; their narrow ends facing each other just below the bulliform cells, in the center of the intercostal zones and separated by 3 or 4 chlorenchyma cells; usually 208–237 microns in horizontal and 22–29 microns in vertical, diameter.

Bulliform Cells: Alternating with all bundles and forming regular groups 3 or 4 cells wide, some more nearly fan-shaped, mainly those flanking the midrib; the groups consisting of large, inflated and thick-walled cells of rather uniform size; groups extending rather deeply into the mesophyll to about half of the blade thickness.

Olyroid Type of Siliceous Cell

We have adopted the term "olyroid type" of siliceous cell or silica body to refer to this special type as found so commonly in the leaf epidermis of the Olyreae (Figures 17, 18). We have found it in all of the species of *Olyra* and related genera which we have studied to the present and illustrated it previously (Calderón and Soderstrom, 1967). These cells were first recognized in the leaf epidermis of *Olyra latifolia* by Grob (1896:48) who called them *Olyrazellen*. These cells could also be designated as "crenate-horizontal." We have assumed that the word horizontal or transversal refers to any axis in right angle to the main or longitudinal axis of the leaf. In this respect our description of the olyroid type of siliceous cell differs from those given by Metcalfe (1960: xix, xlii), who refers to them as "tall, narrow and crenate," or "crenate-vertical." These cells are not exclusive to the Olyreae, however, as they also occur in the epidermis of many species of *Pariana* (Taka Tateoka, 1961) and in some bamboos as well.

The Bambusoid Type of Leaf Anatomy

Grass leaf anatomy, as revealed by features of the transverse sections and epidermal structure, has been the subject of numerous investigations in connection with systematics. The results of these studies have led to the establishment of a number of anatomical types such as the festucoid, panicoid, eragrostoid. The anatomical structure of the leaf of *Maclurolyra* conforms most closely to that of *Olyra* and related genera, traditionally included in the tribe Olyreae, the morphological and anatomical features of which we briefly summarized earlier (Calderón and Soderstrom, 1967). Besides *Olyra* and *Maclurolyra,* included provisionally in this tribe are *Bulbulus, Cryptochloa, Diandrolyra, Ekmanochloa, Lithachne, Mniochloa, Piresia, Raddia, Raddiella,* and *Reitzia.* Related to the Olyreae, and sharing many anatomical features, are the genera *Anomochloa, Buergersiochloa, Eremitis, Froesiochloa, Pariana,* and *Streptochaeta.*

With some minor variations, the genera listed above exhibit most of the features common in the leaves of bamboos. The outstanding feature of these grasses is their herbaceous nature while the bamboos are woody. The anatomical features common to all of the genera, whether herbaceous or woody, make it evident that they form a natural group within the family and should be included in the same subfamily Bambusoideae. For convenience, we refer to grasses of this subfamily as "bambusoid grasses," and to distinguish the two types further, "woody bambusoid grasses" (bamboos) and "herbaceous bambusoid grasses."

The anatomical and histological characteristics of the leaves of bambusoid grasses (mostly bamboos) have received attention from several authors, one of the earliest of whom was Karelstschicoff (1868). More recent anatomical studies have been carried out by Page (1947) and Jacques-Félix (1955a). The most extensive studies are those of Metcalfe (1956, 1960). Most of these papers have dealt with the species of one genus or a few genera, although the number of species of bamboos alone has been estimated at about a thousand (McClure, 1966:288). A number of additional papers can be mentioned which deal with the anatomy of bamboos, although the following list does not pretend to be complete. Some of these papers contain only a few data while others are monographic: Haberlandt (1880, 1882); Güntz (1886); Schwendener (1890); Grob (1896); Wendehake (1901); Brandis (1907); Krause (1909); Takenouchi (1931a, 1931b); Ohki (1932); Hayata (1929); Avdulov (1931); Arber (1934); Prat (1931, 1936); Porterfield (1937); Freier (1941, 1945, 1959); Jacques-Félix (1962); Tuguo Tateoka (1956b, 1957, 1958a); Tateoka, Inoue, and Kawano (1959); Wu (1958, 1960, 1962); Brown (1958); Calderón and Soderstrom (1967). There are several more papers on anatomy of the root, culm, and floral parts, which are not included here.

Our review of the literature and studies of the anatomy of many bambusoid grasses, both woody and herbaceous, indicate that the "bambusoid type" of leaf anatomy may be characterized as follows:

Leaf Blade flat, often asymmetrical, with a very conspicuous *midrib,* containing a complex vascular system; *vascular bundles* usually in two lines and associated with strongly developed sclerenchyma and a ground tissue composed of large cells which contain plastids.

Chlorenchyma not radiate, but mesophyll elements (arm cells and fusoid cells) arranged in horizontal layers parallel to the epidermis.

Arm Cells arranged in a few layers adjacent to both epidermises.

Fusoid Cells almost without exception present, occurring on both sides of the outer bundle sheath and between the arm cells.

Bundle Sheaths always double and well developed; outer, or parenchyma sheath, composed of large cells usually with very few chloroplasts; inner, or mestome sheath, conspicuous, with cell walls uniformly thickened, sometimes more than one layer of cells present.

Small Vascular Bundles usually not angular in outline; sometimes the vertical sides of the outer sheath somewhat parallel (the "leptaspis" type of Metcalfe, 1960).

Sclerenchyma usually forming adaxial and abaxial girders rather than strands; no continuous hypodermal strands have been described.

Transverse Veinlets connecting the longitudinal vascular bundles almost always present.

Epidermis with short cells generally in pairs or sometimes in short rows over the veins.

Silica Bodies over the veins usually saddle-shaped but a variety of forms may occur—cross-shaped, oryzoid type, or intermediate forms; silica bodies between the veins generally of the same shape but transversally narrower or olyroid type.

Microhairs nearly always present and bicellular with both cells of about the same length and uniform in diameter; the distal cell with rounded apex; 3– or 4–cellular microhairs may occur.

Papillae very common and abundant on the long cells; frequently some of them bent toward (overarching) the stomata and obscuring their outline.

Long Cells with thick and very sinuous anticlinal walls.

Stomata usually with low dome-shaped or sometimes triangular subsidiary cells.

Variations in the occurrence and distribution of the characters listed above may occur as is to be expected in any large group. For instance, *Merostachys riedeliana,* as described by Metcalfe (1956), is said to differ from the other bamboos in having no well-defined midrib. The same author illustrates two other species, *Arundinaria murielae and Chusquea abietifolia,* with a comparatively simple vascular system in the midrib, a condition which we have also noted in our own material of *Chimonobambusa densifolia.* Fusoid cells, which are characteristic of the mesophyll of bamboos, were not observed in certain species of *Phyllostachys.* Uniseriate microhairs have been reported for *Guaduella oblonga,* and figured as having 3–6 cells (Jacques-Félix, 1955a; Metcalfe, 1960); also 3–cellular microhairs have been noted for *Arundinaria vagans.* Brandis (1907:80) indicated the presence of soft, pluricellular hairs in the leaf epidermis of *Melocanna bambusoides.* On the other hand, Jacques-Félix (1955a) refers to *Atractocarpa* as lacking microhairs and papillae. In spite of these variations, which are exceptional, the leaf structure of the Bambusoideae seems to be remarkably homogeneous at the generic level. On the whole, the bambusoid grasses have a very distinctive type of mesophyll which makes them stand apart from all other grasses.

From the above description, it is clear that bambusoid grasses exhibit certain anatomical features which are shared by some genera of the Oryzoideae. Members of the tribe Zizanieae Hitchcock (1920:2) and the genera *Chikusichloa, Hygroryza,* and *Rhynchoryza,* like the bamboos, have a complex system of vascular bundles in the midrib; mesophyll composed of fusoid cells and arm cells, although somewhat different; bundle sheath double; and epidermis frequently papillose with oryzoid type silica bodies and often with threadlike microhairs. The resemblance of the bamboos to the Oryzeae, with regard to leaf structure, has been pointed out by several authors (de Winter, 1951; Metcalf, 1960; Tateoka, 1963; Prat, 1931, 1960; Jacques-Félix, 1955b; Schweickerdt and Marais, 1956). However, a sufficient number of differences in the structure of the mesophyll cells, midrib, the predominance of oryzoid type siliceous cells in the epidermis, and the overall gross morphology of the oryzoid grasses

show that, although they are apparently closely related to the bambusoid grasses, they are a distinct group.

Many bambusoid features are also found in the genera *Leptaspis* and *Pharus,* included by some in the tribe Phareae and by others in the subfamily Pharoideae Beetle. But a number of morphological features apparently peculiar to them indicate an isolated position in the family. Until we have studied them further, we prefer not to assign these genera at this time to the Bambusoideae.

The Vascular Bundle Sheath in Grasses

Among the features that investigators of grass leaf anatomy have considered to be of taxonomic significance are the sheaths that surround the vascular bundles. The characters of diagnostic value taken into account are the occurrence of one or two sheaths, i.e., an inner or mestome sheath (Schwendener, 1890) and an outer or parenchyma sheath. When there is only one sheath it is the latter that is present. The degree of development of the cells of the sheaths, the occurrence of chloroplasts in the outer sheath, and whether these are of a specialized type, also have taxonomic importance.

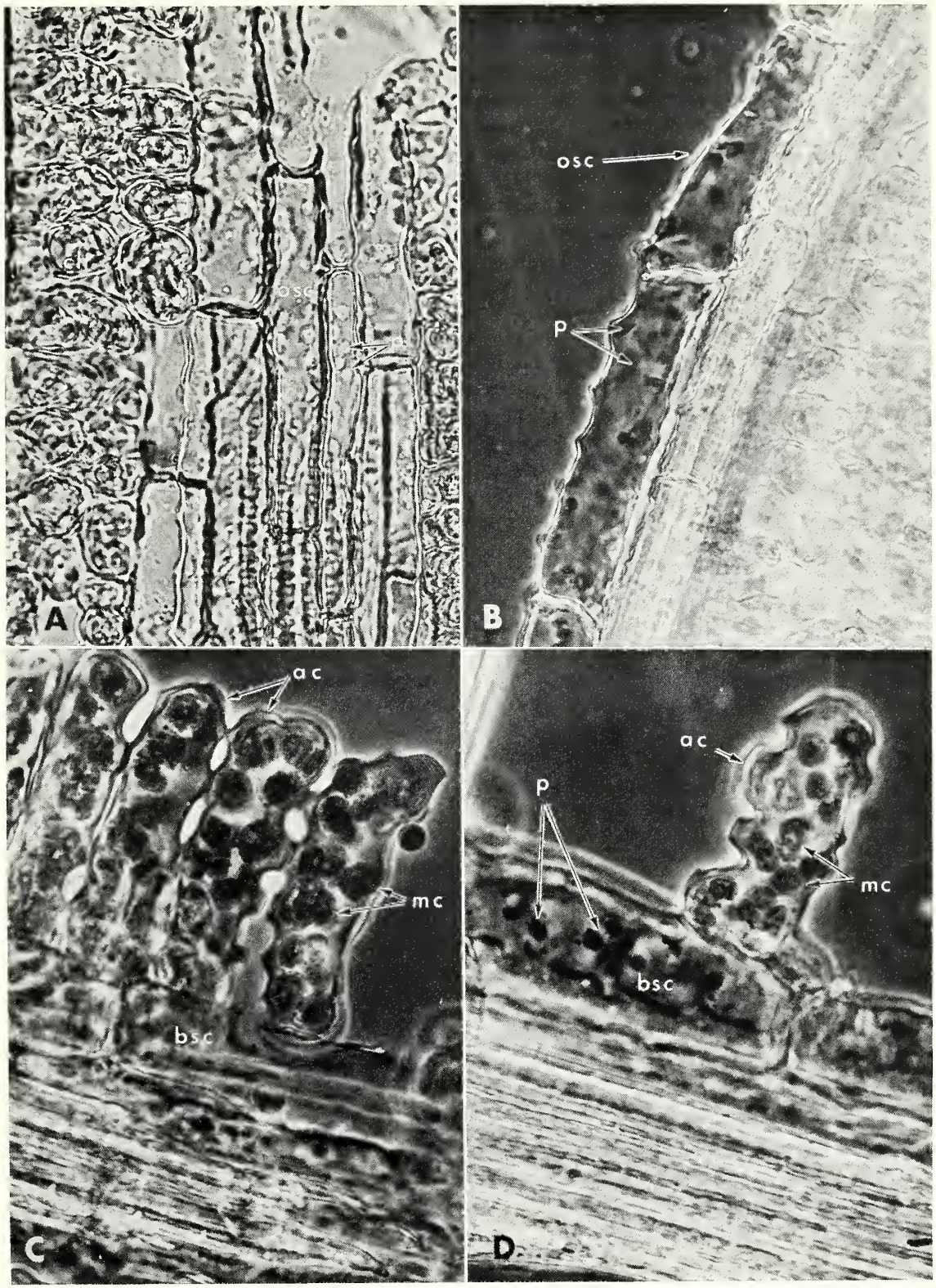
A single sheath is generally characteristic of grasses belonging to the chloridoid-eragrostoid and panicoid groups. The cells of the parenchyma sheath in these groups are large and the chloroplasts are abundant and of a specialized type. Grasses belonging to the festucoid group have two sheaths, a well-developed inner sheath and an indistinct outer sheath composed of thin-walled cells which contain few chloroplasts, these being similar to those of the mesophyll cells. Double sheaths are also found in grasses belonging to the phragmitoid group but the outer sheath has been described as colorless (i.e., without chloroplasts). Grasses of the oryzoid and bambusoid groups possess two well-developed sheaths, but there is little information in the literature regarding their outer sheath and the descriptions themselves are not in agreement. According to Tateoka (1956b) chloroplasts are lacking in the cells of the outer sheath of the Bambuseae, but he presented no further data in support of this statement. Brandis (1907) indicated that in some bamboos the outer sheath has chloroplasts and in others it is colorless. Brown (1958, 1961) concluded that the outer sheath in bambusoid grasses contains chloroplasts, basing this statement on the results of studies of three genera (apparently only one species of each) of bambusoid grasses (*Arundinaria, Phyllostachys,* and *Streptochaeta*). These features of the vascular bundle sheaths were emphasized by Brown, who divided grasses into six major groups according to leaf anatomy. As a result of relying principally on these characters—without consideration of many others—his "bambusoid" type includes many genera which are not closely related.

If one takes into consideration characters of the leaf epidermis, bundle sheaths, mesophyll arrangement, type of chlorenchyma cells, presence or absence of fusoid cells, along with other morphological characters, it is clear that there is no close relationship between such grasses as *Stipa, Uniola, Danthonia,* and the Bambuseae, all of which Brown included in his bambusoid type. The Oryzoideae, which are also included by Brown in his bambusoid type, are certainly near the Bambusoideae, but the oryzoid type of leaf anatomy can easily be separated from the bambusoid. Similar controversial opinions are found in the literature regarding the presence or absence of plastids in the outer sheath of the Oryzoideae. Duval-Jouve (1875) and Tateoka (1956a) refer to the outer bundle sheath of the Oryzeae as colorless while Brown (1958) reports the same sheath as containing chloroplasts.

In the species of bamboos which we have studied, and in all of the genera of Olyreae, we have observed the presence of plastids in the cells of the outer bundle sheath. Even though plastids are present, however, they are often relatively few in number and usually of a very light green color.

In *Maclurolyra* there are two bundle sheaths (Figures 19, 20). The outer bundle sheath is composed of rather large, parenchymatous cells with somewhat thickened walls. These cells are larger in diameter than those of the inner sheath, and they

FIGURE 22.—Photomicrographs of cellular structures of the leaf of *Maclurolyra tecta,* all taken at ×600: A, Longitudinal section through the outer bundle sheath; B, outer bundle sheath cells in a partially dissociated tissue, still attached to the bundle, C and D, partially dissociated tissues showing arm cells viewed from below and bundle sheath cells, respectively. [*ac*=arm cells, *bsc*=bundle sheath cell, *ch*=chlorenchyma, *mc*=mesophyll chloroplast, *osc*=outer sheath cell, *p*=plastids.] Photomicrograph A was taken with bright field illumination, B-D with phase contrast.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are roundish to more or less oval-shaped in cross-section (Figure 21*b*). Study of longitudinal sections shows that they are fairly elongated although they vary in length (Figure 22*a*). In paradermal preparations the sheath cells are found to be in intimate contact with the fusoid cells and their outer tangential wall, when in contact with fusoid cells, is undulated (Figure 22*b*). Bundle sheath cells and those cells which extend the sheath on the adaxial side of the bundle contain plastids (Figure 22*b,d*), although in less amount than in the arm cells.

Transverse veinlets ("cross veins") are also furnished with a bundle sheath (Figure 23 *a-c*). As seen in partially dissociated material they exhibit an entirely different aspect compared with that of the sheath cells of the main veins. They are parenchymatous cells tightly appressed to the veinlets, narrow, very long and usually with rounded or tapered ends. They measure about one-half the length of the transverse veinlet. Sometimes 1 or a few short mesophyll cells connect two long sheath cells in a position toward the middle of the veinlet. Usually the sheath is single along the veinlet but sometimes is partially double (Figure 23*a,b*). The sheath cells of the veinlet are also supplied with chloroplasts which appear to be similar to those of the mesophyll.

As we pointed out in the description of *Maclurolyra,* the inner sheath is very conspicuous and in many vascular bundles double, and seems to be devoid of chloroplasts (Figure 19). The inner sheath cells, as seen in cross-section, have strongly and uniformly thickened walls (Figure 21*a,b*). These features were pointed out earlier by Brandis (1907:77). He remarked that the inner sheath in bamboos is uniformly present, made up of very thick and strongly lignified cell walls, and often consists of several layers. Hayata (1929:32) also remarked that the inner sheath of the bamboos studied by him is strongly developed. We have found this feature to be constant in all genera of the Olyreae (in those genera with several species, at least two or three have been examined); and also in *Pariana, Streptochaeta, Pharus,* and in several species of Bambuseae. On the basis of this survey—in which we have observed no exceptions—we find it tempting to assume that this feature is characteristic of all grasses which belong to the Bambusoideae.

In the festucoid grasses, as in the bambusoid grasses, the inner sheath is well developed. We should stress that the two groups are similar in having a well-developed inner sheath, but the cells which make up the sheaths in each group are quite different. The inner sheath cells in the bambusoid grasses are uniformly thickened. In the festucoid grasses the cells are more strongly thickened on their inner tangential and radial walls than elsewhere, appearing in transverse section as U-shaped (figured in Esau, 1965:439).

Recently Bisalputra, Downton, and Tregunna (1969) have recorded, in electron microscope studies, the presence of plastids in the cells of the mestome sheath of wheat (*Triticum aestivum*), a festucoid grass. The plastids were described as extremely small and appearing to be similar to proplastids.

Chloroplast Structure and Photosynthetic Pathways

In recent years the study of chloroplasts of Gramineae has received special attention, especially in members of the panicoid-chloridoid-eragrostoid lines. It has long been known that in grasses such as corn (*Zea mays*), sugarcane (*Saccharum officinarum*), and sorghum (*Sorghum bicolor*), the cholorplasts of the bundle sheath differ from those of the mesophyll cells, in size, color, and in starch formation and storage capacity (Rhoades and Carvalho, 1944).

The fine structure of the chloroplast is also well known. The chloroplasts of the bundle sheath are different in structure from those of the mesophyll cells (Laetsch, Stetler, and Vlitos, 1965; Laetsch and Price, 1969). They are larger and lighter in color, lack grana or only few are developed, and they contain large amounts of starch. Mesophyll chloroplasts have well-developed grana and contain very small amounts of starch.

Further research has demonstrated that a close correlation exists between leaf anatomy, chloroplast

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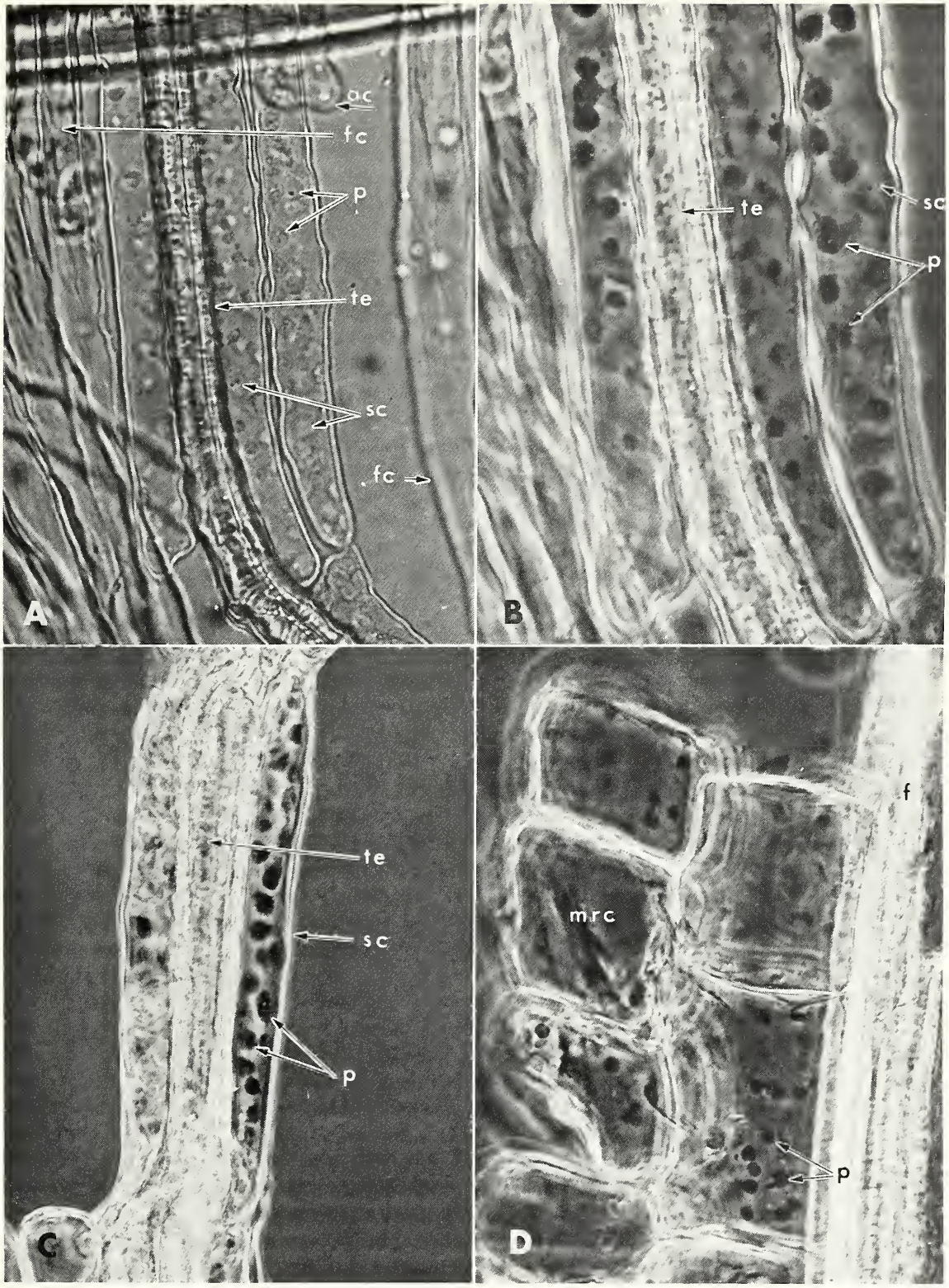
FIGURE 23.—Photomicrographs of cellular structure of the leaf of *Maclurolyra tecta,* all taken at ×600: A-C, Paradermal sections through transverse veinlets showing bundle sheath cells; D, paradermal section of part of the midrib. [*ac*=arm cell, *f*=fibers, *fc*=fusoid cell, *mrc*=midrib cell, *p*=plastids, *sc*=sheath cells, *te*=tracheary elements.] Photomicrograph A was taken with bright field illumination, B-D with phase contrast.


ac
fc
p
te
sc
fc
A
te
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B
te
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C
f
mrc
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D

ultrastructure, and the physiology and biochemistry of photosynthesis (Laetsch, 1969; Tregunna et al., 1970).

In grasses which possess a panicoid type of leaf anatomy (corn, sugarcane, etc.) and specialized sheath chloroplasts, the photosynthetic CO_2 fixation follows a pathway in which C_4-dicarboxylic acids are initial products (Hatch and Slack, 1966). These species have been reported to have very high photosynthetic rates and an apparent lack of photorespiration, features which are also associated with low CO_2 compensation values (Downton and Tregunna, 1968) and low ^{13}C discrimination. Moreover, a lowering of the oxygen concentration around these plants does not enhance the photosynthetic CO_2 assimilation.

Grasses which possess a festucoid type of mesophyll arrangement, on the other hand, are markedly different with respect to the above structural and physiological features. The carboxylation sequence followed by grasses of this group is the conventional Calvin cycle where C–3 compounds are the major initial products. These grasses have low photosynthetic rates and undergo photorespiration. Furthermore, high CO_2 compensation values have also been found in species of this group. In festucoid grasses, the chloroplasts of the sheath cells are similar to those of the mesophyll cells except that they are somewhat smaller in size. Small amounts of starch are found in the mesophyll as well as in the sheath plastids. One of the most recent studies of the ultrastructure of chloroplasts in a festucoid grass was made on wheat (*Triticum aestivum*) by Bisalputra, Downton, and Tregunna (1969). The groups of grasses that possess the anatomical and physiological set of properties found in festucoid grasses are the following natural groups: festucoid (*Festuca, Triticum,* and allies), phragmitoid (*Cortaderia* and allies), oryzoid (*Oryza* and allies), and bambusoid (*Bambusa* and allies).

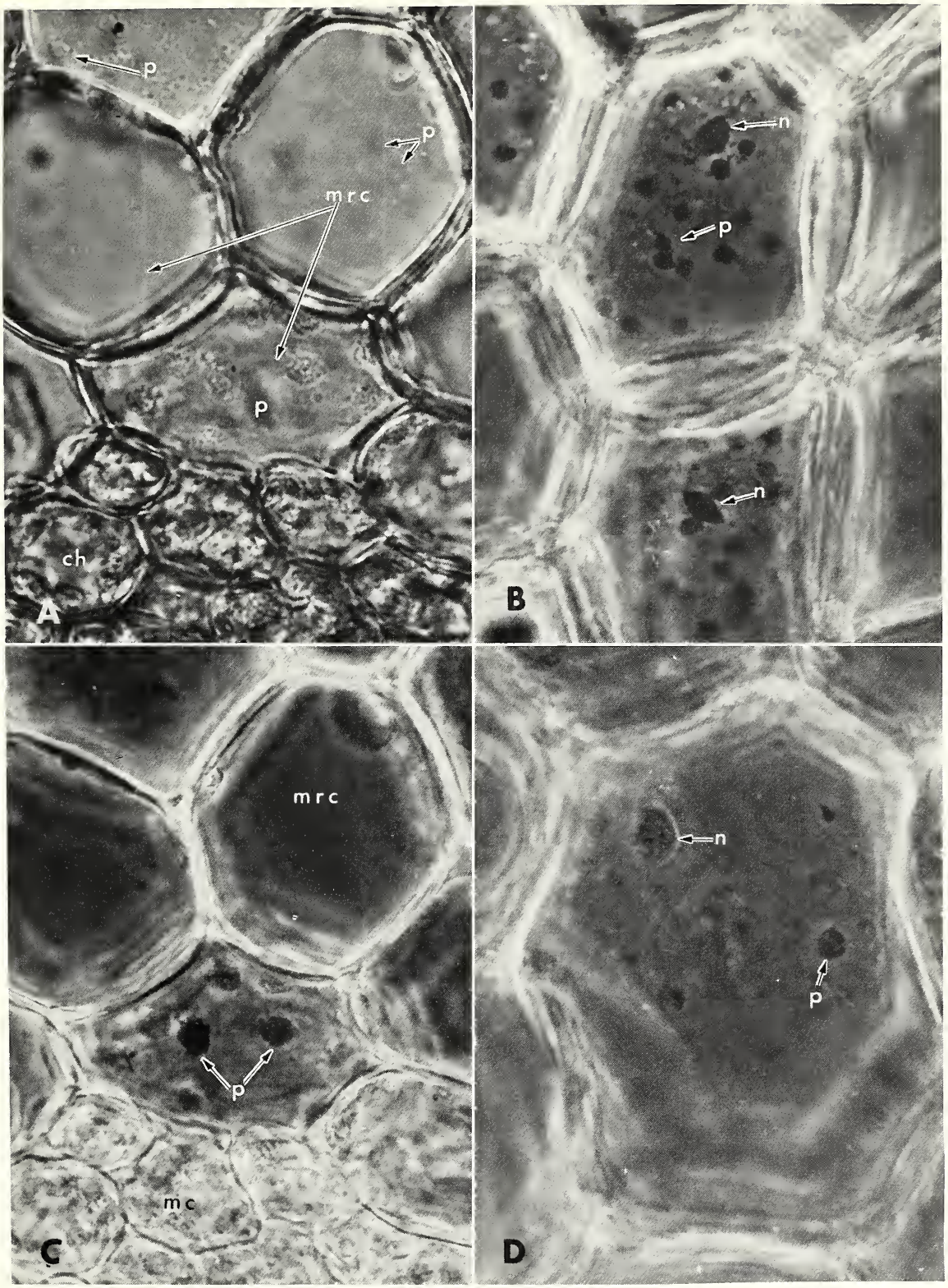
The bambusoid group is included here on the basis of data of CO_2 compensation (in relation to ^{14}C labeling of the C–4 compounds) derived by Hatch, Slack, and Johnson (1967) from *Bambusa vulgaris* and CO_2 compensation values measured by Downton and Tregunna (1968) in an unidentified species of *Bambusa*. To our knowledge no studies have been made on the ultrastructure of chloroplasts of bambusoid grasses.

The striking correlation which exists between the type of physiology and biochemistry of photosynthesis, and mesophyll arrangement, in grasses presents agrostologists with important new characters previously unemployed in the systematics of the family. It is obvious that the study of the photosynthetic apparatus is one of primary importance to the interpretation of the natural lines of the Gramineae. Although our own studies have been limited by light microscopy, we can at least describe the features of the chloroplasts and their distribution in the leaf of one bambusoid grass, *Maclurolyra*. In this genus, we have found plastids not only in the mesophyll and outer bundle sheath, where expected, but also in the cells of the ground tissue of the midrib. Although no physiological data are available for *Maclurolyra*, all evidence from its leaf anatomy would suggest the presence of a C_3 pathway of CO_2 fixation.

Chloroplasts of the Bundle Sheath and Mesophyll.—The chloroplasts of the bundle sheath cells are located within the peripheral cytoplasm. They are round or ovoid and are approximately 3–4 microns long. These dimensions are somewhat smaller than those of the mesophyll arm cells. The bundle sheath plastids are very light green in color and appear somewhat homogeneous in structure (Figure 22*a*). These features can be observed best with phase-contrast illumination (Figure 22*b,d*). On the other hand, the mesophyll arm cells are packed with chloroplasts (Figures 21*b,c*, 22*a,c,d*) which appear to be of the common type, i.e., they are green-colored and of a markedly granular structure. They measure between 5 and 9 microns and are more or less ovoid but tend to vary in their form due to pressure upon each other.

Plastids of the Ground Tissue of the Midrib.—Presence of plastids in the leaf blade is not restricted to the arm cells and parenchyma sheath cells. The cells of the ground tissue, which occupy a large portion of the midrib, also contain plastids. We have found no account in the literature of such

Figure 24.—Photomicrographs of midrib cells of *Maclurolyra tecta*: A, Ground tissue cells adjacent to the chlorenchyma showing transition between them and the plastids of the central ground tissue; B, ground tissue cells with plastids; C, same as A but under different illumination; D, single cell of the ground tissue. [*ch*=chlorenchyma, *mc*=mesophyll cell, *mrc*=midrib cell, *n*=nucleus, *p*=plastids.] Photomicrograph A taken with bright field illumination; B-D with phase contrast. Magnifications: A-C, ×600; D, ×1250.


p
p
mrc
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ch
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D

plastids in the ground tissue (frequently referred to as "colorless tissue"). The ground tissue plastids differ from those of the nearby mesophyll in that they are very small and almost translucent (Figure 24*a*). The former are roundish in cross-section and measure approximately 2.5 to 3.5 microns in length. There are relatively few plastids per cell, and these occur usually near the walls and sometimes around the nucleus. In cross-section (Figure 24*b,d*) only very few of them are seen in some of the cells, but paradermal or longitudinal sections reveal their presence in all of the cells (Figure 23*d*). These plastids are extremely light colored when observed under regular transmitted light. They are more or less similar to the bundle sheath plastids and show a homogeneous structure. The number of plastids per cell and their size and color increase in those cells of the ground tissue which are near or adjacent to the arm cells of the midrib (Figure 24*a,c*). This gradual differentiation of the midrib organelles suggests that these are plastids, probably similar to preplastids. Sections treated with a weak IKI solution did not stain, indicating that no large amounts of starch are deposited in these organelles. We have also observed such plastids in the midrib of all of the genera of the Olyreae, *Pariana, Pharus, Streptochaeta,* and in several bamboos, as enumerated in the following list. Except for slight differences in size, color, and abundance, all of these species have plastids in the ground tissue of the midrib:

Bambusa arundinacea (*Soderstrom & Kulatunge* 1774), *B. multiplex* (*Soderstrom & Kulatunge* 1603), *B. vulgaris* (*Soderstrom & Kulatunge* 1763), *Chimonobambusa densifolia* (*Soderstrom & Kulatunge* 1656), *Cryptochloa* species (*Calderón* 2074, 2083), *Dendrocalamus giganteus* (*Soderstrom & Kulatunge* 1602), *Diandrolyra bicolor* (*Soderstrom* s.n.), *Eremitis monothalamia* (*Calderón* 2039), *Indocalamus debilis* (*Soderstrom & Kulatunge* 1606), *I. floribundus* (*Soderstrom & Kulatunge* 1658), *I. walkerianus* (*Soderstrom & Kulatunge* 1772), *I. wightianus* (*Soderstrom & Kulatunge* 1608), *Lithachne pauciflora* (*Pohl & Calderón* 10136), *Ochlandra stridula* (*Soderstrom & Kulatunge* 1673), *Olyra fasciculata* (*Calderón* 2024), *O. glaberrima* (*Calderón* 2010), *O. lateralis* (*Calderón* 2092), *O. obliquifolia* (*Calderón* 2062), *O.* aff. *taquara* (*Calderón* 2087), *Oxytenanthera monadelpha* (*Soderstrom & Kulatunge* 1605), *Pariana campestris* (*Calderón* 2063), *P. lanceolata* (*Calderón* 2040), *Pharus* species (*Soderstrom & Calderón* 1206), *P. glaber* (*Calderón* 2016), *Piresia goeldii* (*Soderstrom* 1428), *Piresia* species (*Calderón* 2047), *Raddia brasiliensis* (*Calderón* 2031), *R. costaricensis* (*Calderón* 2109), *Raddiella nana* (*Calderón* 2009, 2071), *Reitzia smithii* (*Calderón* 2002), *Streptochaeta sodiroana* (*Soderstrom & Calderón* 1205), and *Teinostachyum attenuatum* (*Soderstrom & Kulatunge* 1657).

Phylogenetic Position of *Maclurolyra*

Probably the best clue to the relationships of an unknown grass is found in its leaf anatomy and epidermis. Thus the first step in determining the phylogenetic position of *Maclurolyra* was a study of these aspects of the plant. We found its leaf blade to contain a mesophyll composed of fusoid cells and arm cells arranged in layers parallel to the epidermis, two well-developed bundle sheaths with the outer one containing chloroplasts, and a fairly complex midrib structure—with an epidermis containing saddle-shaped and olyroid type siliceous cells, bicellular microhairs, an abundance of papillae, and stomata with triangular subsidiary cells.

Such a leaf structure is characteristic of bamboos, a group of grasses traditionally regarded as rather distinct within the family, doubtless due to the woody nature of their culms and a number of morphological features not ordinarily found in other grasses. A few grasses with herbaceous culms have been studied by other investigators who found them to have the same type of leaf anatomy, and the suggestion has been made that some might belong to the same subfamily as the bamboos. Our comparative studies of the leaf anatomy of *Maclurolyra,* of a number of bamboos, and of the putatively allied herbaceous genera, have led us to the conclusion that all possess a rather homogeneous leaf anatomy and should indeed be included within the same subfamily, Bambusoideae. The "bambusoid" type of leaf anatomy, which we have attempted to clarify, is found not only in the largest of bamboos, such as *Dendrocalamus giganteus,* whose culms may ascend to thirty meters, but as well in such Lilliputian members as *Raddiella nana,* whose culms reach no higher than a few centimeters.

In addition to its leaf anatomy, several other features of *Maclurolyra* recall those which are com-

mon among bamboos: rhizomatous nature, petiolate leaf with a broad blade and tessellate venation; three vascularized lodicules; hairs on the style; high basic chromosome number; small embryo; linear hilum. Even the seedling of *Maclurolyra* is like that of the bamboos, characterized by the development of one or more reduced leaves before the first expanded blade, which is broad, ovate-lanceolate, and held in a horizontal position.

The herbaceous condition of the culm of *Maclurolyra tecta,* its 1–flowered spikelets, and monoecious condition, all point to a relationship—within the Bambusoideae—to the tribe Olyreae. In genera of this tribe, the female spikelets are 1–flowered and consist of two glumes, an indurate lemma and palea, 3 lodicules, and a gynoecium with a single long style and 2 stigmas. The male spikelet is also 1–flowered and consists generally of a thin 3–nerved lemma and palea, 3 lodicules, and an androecium of 3 stamens, but usually lacks glumes. Occasionally the female spikelet contains rudiments of male organs in the form of staminodes, and the male spikelet contains rudiments of the female organ in the form of a pistilodium.

The spikelet arrangement in *Maclurolyra* and the multinerved condition of the male lemma are repeated in the genus *Bulbulus.* Both genera are also consistent in the presence of a pistilodium in the male flower and staminodes in the female flower.

Separation of sexes, with the concomitant monoecious or dioecious condition, is regarded as a highly advanced floral character in the angiosperms. The presence of staminodes in the female flowers and pistilodium in the male flowers of some Olyreae is an indication that they were once bisexual. Although the monoecious condition is found in all genera of the Olyreae, it is rare elsewhere in the Bambusoideae.

It is interesting to note that separation of sexes has occurred in the most advanced members of all of the large major natural groups of the grass family: festucoid group (section Dioicopoa of the genus *Poa*), centothecoid group (*Zeugites*), chloridoid-eragrostoid group (*Buchlomimus, Reederochloa*), phragmitoid group (*Phragmites*), oryzoid group (*Hygroryza, Luziola, Zizania*), panicoid group (tribe Andropogoneae, tribe Tripsacaceae, *Spinifex*). Therefore, with respect to the character of monoecism, the Olyreae seem to represent an advanced line of the bambusoid group.

Because the monoecious condition is found in each natural group of grasses, it must have occurred independently in each line. Considering this condition to have arisen only once and to be of primary importance, led Roberty (1960:36–37) to bring together such widely unrelated monoecious genera as *Olyra* and *Zea* and to consider them to belong to an entirely separate family, the Zeaceae (!).

Reduction in the number of vascular traces in the ovule of bambusoid grasses appears to be an indication of advancement. In the genus *Streptochaeta,* Arber (1929:41) noted the presence of four vascular traces, a condition common in many bamboos. In other bamboos five or six traces have been recorded. It is tempting to consider the condition of three traces as found in the ovule of *Maclurolyra* and other Olyreae as an advancement over those in which the number is larger.

Maclurolyra tecta is a diploid with a basic number of $x = 11$, the most common basic number in the Olyreae. However, the basic number for the subfamily Bambusoideae is $x = 12$, with this number reported for the herbaceous genera *Pariana* and *Streptogyna,* and for the majority of bamboos. The basic number of $x = 12$ is also found in many genera of other grass groups such as the oryzoid, phragmitoid, and centothecoid. This supports the viewpoint of Tzveliov (1969), who states that $x = 12$ is the basic number for the grass family. Tzveliov further postulates that lower basic numbers in the family are derived from $x = 12$.

Within the Bambusoideae, the Olyreae may thus be regarded as advanced in terms of their basic chromosome number. Although $x = 11$ is the most common basic number we have encountered so far in the tribe, we have found numbers as low as $x = 7$. Within the tribe itself, *Maclurolyra* might be among the least advanced genera since it retains the basic number of 11. It is interesting to point out that most bamboos are tetraploids ($2n=48$), which is the most widespread level of polyploidy in the great majority of mature polyploid complexes, according to Stebbins (1971:162).

As we stated earlier (Soderstrom and Calderón, 1971), bamboos probably were derived fom herbaceous ancestors. It is probable that bamboos arose as polyploids from diploid herbaceous ancestors, perhaps on more than one occasion. Their success as polyploids must certainly be attributed to

the fact that they are long-lived perennials, with strongly developed rhizomes that allow them to reproduce vegetatively. Flowering in most bamboos is infrequent and when it occurs, sterility barriers are often present.

Most herbaceous bambusoid grasses are diploid and flower throughout the year, while most bamboos are tetraploid and flower only once in many years. Over a long period of time the former produce countless generations in comparison with the latter, a point commented upon by Arber (1934: 87). This has allowed specialization to occur in the spikelet structure of the herbaceous bambusoid grasses while the same has apparently occurred to a lesser extent in the bamboos.

Recent studies have shown that angiosperms are separable into two groups with regard to their photosynthetic carbon metabolism. The predominance of a C_3 or C_4 pathway is associated with a set of distinct photosynthetic properties and particular features of the leaf anatomy, chloroplast ultrastructure, and ecology—a correlation which has proved to be consistent with taxonomic groupings. Data concerning any one of these physiological or anatomical characteristics can be used as reliable indicators of the dominant carbon fixation pathway followed by a plant. In *Maclurolyra,* for example, the presence of a C_3 metabolism is suggested by its bambusoid type of leaf anatomy. This less efficient type of metabolism has also been reported for grasses of the oryzoid, festucoid, stipoid, and phragmitoid groups, in contrast to the highly efficient C_4 pathway of photosynthesis found only in the most advanced members of the family.

In conclusion, our studies show that *Maclurolyra* is a genus which belongs to the tribe Olyreae of the subfamily Bambusoideae, and apparently represents one of the less specialized genera of the tribe. It is not surprising that it inhabits rain forests in Panama, an area which is phytogeographically related to the Chocó region of Panama and Colombia, the latter considered to be one of the ancient forests that harbors relic genera (Haffer, 1969).

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Appendix 1

Genera of the Subfamily Bambusoideae Aescherson and Graebner

We consider the subfamily Bambusoideae to comprise the genera in the following list. The list is the result of our consultations concerning the bamboos with the late F. A. McClure and our own studies on herbaceous bambusoid grasses. This list is to be considered provisional since we have not yet studied representatives of each genus. (H) following the name indicates that the genus is an herbaceous bambusoid grass; all others are bamboos.

Anomochloa (H), *Arthrostylidium, Arundinaria, Athroostachys, Aulonemia, Bambusa, Bonia, Brachystachyum, Buergersiochloa* (H), *Bulbulus* (H), *Cephalostachyum, Chimonobambusa, Chusquea, Cryptochloa* (H), *Decaryochloa, Dendrocalamus, Dendrochloa, Diandrolyra* (H), *Dinochloa, Ekmanochloa* (H), *Elytrostachys, Eremitis* (H), *Fargesia, Froesiochloa* (H), *Gigantochloa, Glaziophyton, Greslania, Guadua, Guaduella* (H), *Hickelia, Hitchcockella, Indocalamus, Indosasa, Lingnania, Lithachne* (H), *Maclurolyra* (H), *Melocalamus, Melocanna, Merostachys, Mniochloa* (H), *Myriocladus, Nastus, Neohouzeaua, Neurolepis* (H), *Ochlandra, Olyra* (H), *Oreobambos, Oxytenanthera, Pariana* (H), *Perrierbambus, Phyllostachys, Pinesia* (H), *Pleioblastus, Pseudocoix, Pseudosasa, Pseudostachyum, Puelia* (H), *Racemobambos, Raddia* (H), *Raddiella* (H), *Reitzia* (H), *Rettbergia, Sasa, Sasaella, Sasamorpha, Schizostachyum, Semiarundinaria, Shibataea, Sinarundinaria, Sinobambusa, Sinocalamus, Streptochaeta* (H), *Streptogyna* (H), *Teinostachyum, Thamnocalamus, Thyrsostachys, Yushania.*

Appendix 2

List of Material Studied

Bambusa arundinacea. Ceylon: Kandy District: Peradeniya. 10 December 1969. *Soderstrom & Kulatunge* 1774.

Bambusa multiplex. Ceylon: Kandy District: Peradeniya; Royal Botanic Gardens. 27 October 1969. *Soderstrom & Kulatunge* 1603.

Bambusa vulgaris. Ceylon: Kandy District: near the Malwatte Temple. 1 December 1969. *Soderstrom & Kulatunge* 1763.

Bulbulus nervatus Swallen. Surinam: Wilhelmina Gebergte. 1 September 1963. *Irwin, Prance, Soderstrom, & Holmgren* 55321.

Cephalostachyum burmanicum. USDA (United States Department of Agriculture) P.I. (Plant Introduction) No. 117530.

Chimonobambusa densifolia. Ceylon: Nuwara Eliya District: Horton Plains. 11 November 1969. *Soderstrom & Kulatunge* 1656.

Cryptochloa, new species. Panama: Prov. de Panamá: Cerro Jefe. 3 March 1968. *Calderón* 2074.

Cryptochloa, new species. Panama: Prov. de Panamá: Cerro Jefe. 8 March 1968. *Calderón* 2083.

Dendrocalamus giganteus. Ceylon: Kandy District: Peradeniya; Royal Botanic Gardens. 23 October 1969. *Soderstrom & Kalatunge* 1602.

Diandrolyra bicolor. England: Kew, cultivated at Royal Botanic Gardens. November 1967. *Soderstrom* s.n.

Eremitis monothalamia. Brazil: Bahia: Municipio Ubaitaba. 13 January 1968. *Calderón* 2039.

Indocalamus debilis. Ceylon: Nuwara Eliya District: lower slopes of Pidurutalagala. 3 November 1969. *Soderstrom & Kulatunge* 1606.

Indocalamus floribundus. Ceylon: Badulla District: between Ohiya and Boralanda. 13 November 1969. *Soderstrom & Kulatunge* 1658.

Indocalamus walkerianus. Ceylon: Nuwara Eliya District: near Edikatupana. 5 December 1969. *Soderstrom & Kulatunge* 1772.

Indocalamus wightianus. Ceylon: Nuwara Eliya District: summit of Pidurutalagala. 4 November 1969. *Soderstrom & Kulatunge* 1608.

Lithachne pauciflora. Costa Rica. 1966. *Pohl & Calderón* 10136.

Ochlandra stridula. Ceylon: Kegalle District: Arandara. 16 November 1969. *Soderstrom & Kulatunge* 1673.

Olyra fasciculata. Brazil: Guanabara: Estrada da Gávea. 3 January 1968. *Calderón* 2024.

Olyra glaberrima. Brazil: Guanabara: Rio de Janeiro. 28 December 1967. *Calderón* 2010.

Olyra lateralis. Panama: Prov. de Panamá: Cerro Campana. 13 March 1968. *Calderón* 2092.

Olyra latifolia L. Venezuela: Aragua: Maracay. 18 February 1968. *Calderón* 2072.

Olyra obliquifolia. Brazil: Pará: Belém. 29 January 1968. *Calderón* 2062.

Olyra aff. *taquara.* Panama: Prov. de Panamá: Cerro Azul. 11 March 1968. *Calderón* 2087.

Oxytenanthera monadelpha. Ceylon: Nuwara Eliya District: near Ramboda. 2 November 1969. *Soderstrom & Kulatunge* 1605.

Pariana campestris. Brazil: Pará: Belém. 2 February 1968. *Calderón* 2063.

Pariana lanceolata. Brazil: Bahia: Municipio Ubaitaba. 13 January 1968. *Calderón* 2040.

Pharus sp. Costa Rica: Puntarenas. 27 June 1966. *Soderstrom & Calderón* 1206.

Pharus glaber. Brazil: Guanabara: Rio de Janeiro. 29 December 1968. *Calderón* 2016.

Piresia goeldii. Colombia: Amazonas: Leticia. 4 February 1969. *Soderstrom* 1428.

Piresia, new species. Brazil: Bahia: Santa Cruz Cabralia. 18 January 1968. *Calderón* 2047.

Raddia brasiliensis. Brazil: Bahia: Municipio Ubaitaba. 11 January 1968. *Calderón* 2031.

Raddia costaricensis. Costa Rica: Prov. de Limón: Rio Hondo. 28 March 1968. *Calderón* 2109.

Raddiella nana. Brazil: Distrito Federal: Parque Municipal do Gama. 21 December 1967. *Calderón* 2009. Pará: Municipio Vigía, Campinha do Paiha. 10 February 1968. Calderón 2071.

Reitzia smithii. Brazil: Santa Catarina: Municipio Brusque, Asambuja. 8 December 1967. *Calderón* 2002.

Streptochaeta sodiroana. Costa Rica: Puntarenas. 27 June 1966. *Soderstrom & Calderón* 1205.

Teinostachyum attenuatum. Ceylon: Badulla District: between Horton Plains and Ohiya. 12 November 1969. *Soderstrom & Kulatunge* 1657.

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